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REPRODUCTIVE BIOLOGY OF THE AUSTRALIAN BUSH RAT *RATTUS ASSIMILIS*

BY
J. MARY TAYLOR

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REPRODUCTIVE BIOLOGY OF THE AUSTRALIAN BUSH RAT, *RATTUS ASSIMILIS*

BY

J. MARY TAYLOR

(A contribution from the Museum of Vertebrate Zoology
of the University of California)

INTRODUCTION

IT IS COMMONLY ASSUMED that the mammalian fauna of Australia is composed entirely of the two monotremes, the platypus and the spiny anteater, and the marsupials, which in diverse forms have come to occupy all parts of that continent. Actually, however, there are four orders of mammals native to Australia in addition to the monotremes and marsupials, represented by the dugong, seals, bats, and rodents. All the rodents belong to the true rats of the family Muridae. This family, the only terrestrial group of eutherian mammals native to the continent, is represented there by two subfamilies, thirteen genera, and sixty-seven species (Tate, 1951). The degree of specialization and the number of endemic species within the Australian Muridae suggest that rodents have inhabited the continent for a long period of geological history. Unless the murids have undergone very rapid adaptive radiation from their presumed Asiatic ancestry, it would not be surprising to find their remains in Australia, as far back as the Pliocene.

Wherever marsupials are present on the continent, one or more species of murids are found also. The rodents are actually or potentially competing with marsupials for food and space; as a group they differ conspicuously in mode of living from marsupials only in their manner of reproduction. Of these two mammalian groups, the Muridae are reproductively much more efficient in that they become sexually mature at a far earlier age and produce more generations of young per given unit of time. The actual mode of reproduction may not be less efficient in marsupials (Reynolds, 1952), but their reproductive potential is lower. Undoubtedly, the very high reproductive potential of certain members of the Muridae is one of the reasons for their success in becoming cosmopolitan in distribution since the spread of modern man.

Among the Australian murids there are thirteen endemic species of the genus *Rattus*, all of which show a marked similarity to forms of the Malayan Archipelago and which probably represent the most recent infiltrations of murids into Australia prior to the advent of man. They are the most unspecialized of the native rodents and have the widest geographical range.

Because there were no other terrestrial Eutheria on the Australian continent, Australia must have offered a partial ecological vacuum to rodents when they arrived. Nevertheless, these native rats have not heavily populated the continent, at least not in historical times. The native murids are widespread, to be sure, but under normal circumstances they cannot be considered abundant. In fact, they tend to hold to a density rather lower than one might expect for the murids. Population outbreaks of rodents constitute a common worldwide phenomenon, and the

Australian murids are typical in this respect (Palmer, 1885; Cleland, 1918; Crombie, 1944). Sporadic outbreaks in Australia are recognized in the cane fields of northern Australia and in pine plantations, but as McDougall (1946b:212) points out, "in normal years, even on farms at other times heavily infested, rats exist if at all mostly in low densities."

It can be seen from McDougall's study (1944a, 1944b, 1944c, 1946a, 1946b, 1947, 1950) that the reproductive potential of at least some of the native *Rattus* of Australia is reasonably high, and yet, except for sporadic population peaks, the actual number of rats per given area seems depressed to a level much lower than one would expect the area to be capable of supporting. What form, or forms, this depressant takes and whether it is endogenous or exogenous or both is not suggested by McDougall's ten-year study of *R. conatus*. Extensive knowledge of the breeding biology and ecology of the Australian rodents is essential to formulate answers to these questions.

Accordingly, one of the most common and widespread of the native Australian rodents, *Rattus assimilis*, was chosen in the present study for an investigation of certain aspects of its reproductive biology in the field and under laboratory conditions. *Rattus assimilis* was first described by John Gould in 1857, and later a more detailed morphological analysis of this species was made by Troughton (1920). Now, more than a hundred years after Gould's original description, the present investigation represents, so far as the writer knows, the first long-term study of *R. assimilis* as a living animal.

ACKNOWLEDGMENTS

The field work of this project was made financially possible by a Fulbright Grant to the University of Sydney and by the Fanny Bullock Workman Fellowship from Smith College. Gratitude is expressed to the late Mr. Frank J. Griffiths, Chief Guardian of Fauna of New South Wales, who granted a permit to live-trap mammals and who gave his wholehearted support of this type of work in Australia. I am deeply grateful to Dr. B. Elizabeth Horner, of Smith College, who led our field program in Australia and has offered many valuable suggestions.

For permission to examine specimens, for museum data, and for field information, I wish to thank Mr. C. W. Brazenor of the National Museum of Victoria, Dr. Peter Crowcroft of the British Museum, Dr. J. L. Harrison of the Queensland Institute of Medical Research, Dr. David H. Johnson of the United States National Museum, Dr. A. Gordon Lyne of the Commonwealth Scientific and Industrial Research Organization, Mr. J. McNally of the Fisheries and Game Department of Victoria, Mr. George Mack of the Queensland Museum, Miss Viola Schantz of the United States Fish and Wildlife Service, Mr. Ellis Troughton and Mr. Basil Marlow of the Australian Museum, and Mr. Hobart M. Van Deusen of the American Museum of Natural History.

Mr. Desmond O'Connor and Mr. Rupert Vallentine, of the University of New South Wales, very generously surveyed a segment of the trapping area to show precise locations of traps with reference to contour features of the land.

Dr. Marjorie Nelson gave much valuable advice in the course of the laboratory project. Maintenance of the colony, housing facilities, and equipment were pro-

vided by the Museum of Vertebrate Zoölogy and the Department of Zoölogy, University of California, and by a University of California patent fund grant. Many helpful ideas and suggestions were offered by William J. Maher, to whom I wish to express my sincere thanks. I am indebted to Donald Isaac for assistance in photographic techniques and for care of the rat colony for several weeks. Gene M. Christman gave valuable advice and help in the preparation of the figures.

The project was carried out under the guidance of Dr. Alden H. Miller, to whom I am deeply grateful for his supervision and criticism of the work. I am also especially grateful to Dr. Oliver P. Pearson, Dr. Ruben A. Stirton, and Dr. Francis C. Evans, who have offered much helpful advice.

FIELD STUDY

GEOGRAPHIC DISTRIBUTION

The geographic range of the Allied Rat, *Rattus assimilis*, when described by John Gould in 1857 and again in 1863, was recorded as extending from northeastern Queensland to southwestern Australia. Since the native rodents were for the most part ignored by subsequent scientific investigators and since many of the prepared specimens were housed in foreign museums, writings which followed Gould's descriptions were for many decades largely rewordings of his original interpretation. However, in 1925 Wood Jones wrote that he knew of no recent record of *R. assimilis* in the State of South Australia. He also pointed out that Gould did not recognize *Rattus greyi*, which is widely distributed in South Australia and which is very similar to *R. assimilis* in appearance. With the exception of Ellerman (1949:62), who classified both *greyi* and *assimilis* as subspecies of *Rattus fuscipes*, there is general acceptance of *R. greyi* as a full species. The acknowledgment of *greyi* as a species distinct from *assimilis* has altered the initially recognized range of *assimilis*. Troughton (1954) considered *R. assimilis* to have one of the widest distributions of any member of the genus native to Australia, and gave its range as the forest and mountain areas of eastern Australia from the Atherton Tableland in Queensland to Victoria. Tate (1951:326) recognized a *Rattus assimilis* group within which he included *R. greyi* as a full species. He listed three subspecies of *R. assimilis*: *R. a. assimilis*, found at Gympie, Queensland, and southward to Victoria; *R. a. coracius*, ranging from Cairns and the Atherton Tableland to Paluma Range west of Townsville; and *R. a. manicatus*, which he described from the type specimen collected at Port Essington in the Northern Territory (fig. 1). Troughton (1954) appeared not to recognize the last subspecies.

Owl-pellet specimens from southwestern Western Australia were tentatively assigned to *Rattus assimilis* (Shortridge, 1936), and an immature specimen of *R. assimilis* was recorded from Fiji (Mumford, 1942). The specimen from Fiji, once called *Mus huegeli*, was synonymized with *Rattus exulans* by Tate (1935) and later re-identified by Tate as *R. assimilis* (Mumford, 1942). The one Fijian specimen in existence, taken in the 1890's, "may have been unique or one of a very few [individuals] . . . that failed to become established there." The species "does not appear to have been taken since" (Mumford, 1942:214).

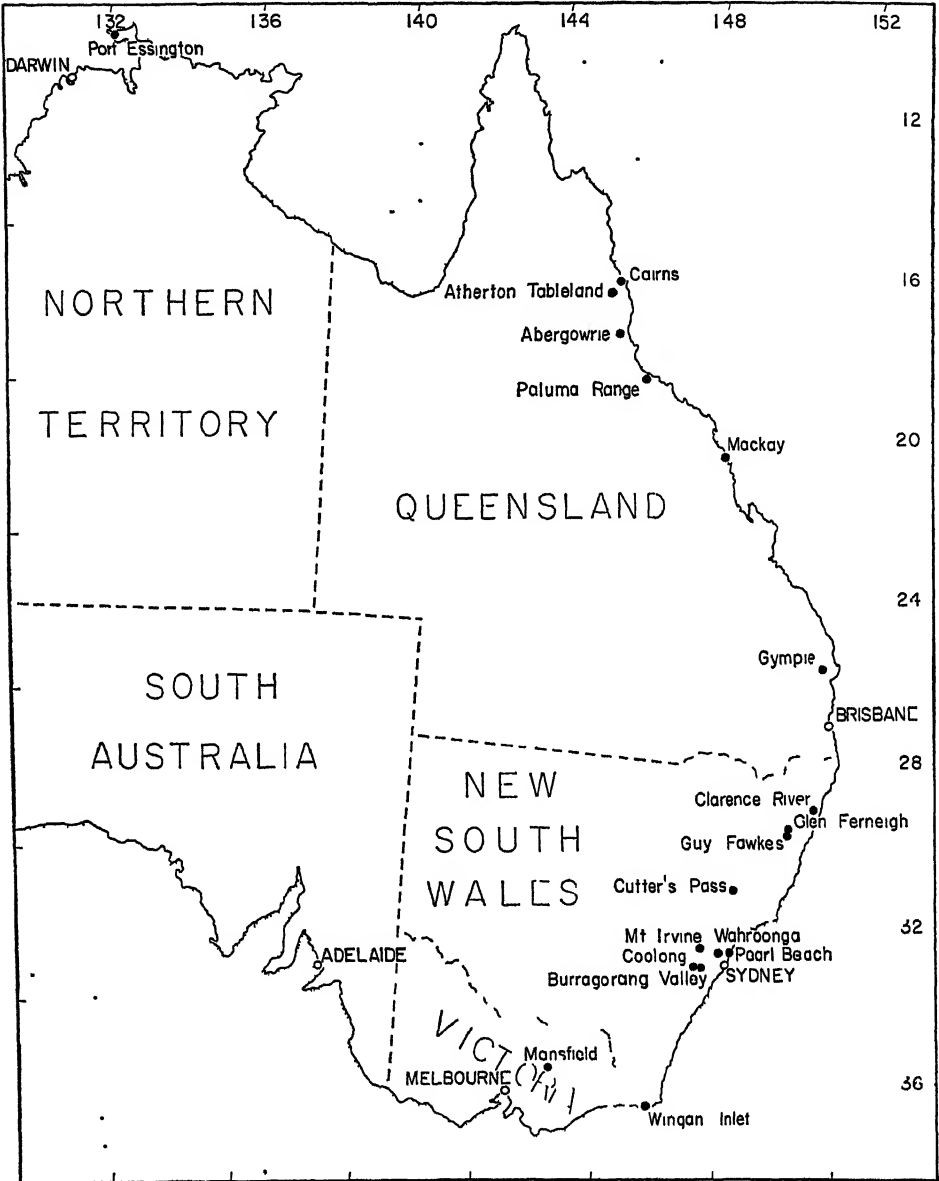


Fig 1. Map of eastern Australia showing localities referred to in text.

There are few published range maps for any of the Australian mammals. Tate (1951), however, described the distribution of the *Rattus assimilis* group as roughly horseshoe-shaped. The present author prefers to omit the very tenuous recognition of *R. a. manicatus* and to visualize the distribution of the species as roughly a band along eastern Australia following the coast and invading inland mountain and forested areas.

The type specimen on which Gould based the species was obtained from the Clarence River in northern New South Wales. This area falls within the range of the subspecies *Rattus assimilis assimilis*. Field work in the present study was carried out at Pearl Beach 300 miles south of the type locality and is well within the present recognized distribution of this subspecies (fig. 1).

STUDY AREA

Certain blocks of Crown Land in Australia are now being set aside as wildlife reserves. The area selected for the present study, Warrah Sanctuary, is such a reserve. At the time of the study, September, 1954, to September, 1955, it consisted of 950 acres.

Warrah Sanctuary lies immediately north of the mouth of the Hawkesbury River in Gostford Shire, New South Wales. The southern border of the Sanctuary, which is the north shore of the Hawkesbury River, is bounded by the towns of Pearl Beach on its eastern limit and Patonga on its western limit (pl. 1). The area lies within an extensive Triassic exposure, the Hawkesbury sandstone group. The group consists mainly of siliceous sandstones and a few small lenticular beds of shale (Pidgeon, 1937). In many places the sandstone along the escarpment has been eroded into large vertical blocks. Warrah Sanctuary is part of a plateau, 700-900 feet high, that extends north of Sydney along the coast and is deeply bisected by a drowned river-valley now occupied by Broken Bay and the Hawkesbury River. Weathering has etched many vertical cliffs and numerous steep gullies into an otherwise rather level land profile. The effect has been to break up the land into a mosaic of habitats. On Warrah Sanctuary alone the altitude varies from sea level to 878 feet, and there are extensive slope exposures in every direction.

The sandy soils, derived from the Hawkesbury sandstones, are typically very shallow and retain little moisture. Harris (1956) maintains that the low moisture-retaining capacity of the soils is a major factor in the dominance of xeromorphic vegetational types, despite the moderately high average yearly rainfall in this district of more than 40 inches. Rainfall is fairly evenly distributed throughout the year, averaging just below 4 inches per month. A slight peak of about 5 inches per month occurs from March through May, and the rainfall drops to about 3 inches per month from August through November.

The average temperature for the Sydney district, in which the study area lies, ranges from a mean minimum of 56.3° F. to a mean maximum of 71.1° F. (Commonwealth of Australia, 1954). The temperature recorded at the study area during the period of field work ranged from a minimum of 33° F. (August 6, 1955) to a maximum of 101° F. (January 3, 1955).

According to Pidgeon (1937), two major types of vegetation are recognized in the central coast region of New South Wales: subtropical rainforest and *Eucalyptus* forest. Rainforest is composed of plants primarily of Indo-Malayan origin (Beadle, 1954) and occurs in pockets, which are considered to be remnants of a formerly more extensive distribution (Pidgeon, 1937), where soils are moist and comparatively rich and where there is protection from desiccating winds. *Eucalyptus* forest, however, is Australian in origin; the major families represented

are Proteaceae, Myrtaceae, Leguminosae, Epacridaceae, and Rutaceae. Of the two vegetational types, *Eucalyptus* forest is by far the more extensive throughout this central coast area.

Warrah Sanctuary is entirely covered with *Eucalyptus* forest, although some of the very moist gullies harbor a few species of the rainforest element (pl. 2, a). One of the most common of these relics (or invaders) is the cabbage-tree palm, *Livistona australis*, a frequent creek-border associate in deep gullies of permanent streams. Even at stream borders, however, vegetation is essentially sclerophyllous and therefore characteristic of the *Eucalyptus* forest vegetational type.

Eucalyptus and *Angophora* are the dominant genera of the upper canopy. In gullies and other protected areas the canopy may attain a maximum height of more than 100 feet. *Angophora* sp. is common here. Tops and exposed slopes of hills characteristically bear an upper canopy of considerably less stature, often averaging less than 40 feet. Here also the trees are usually spaced farther apart. In some exposed areas the *Eucalyptus* element has given way entirely to a low shrub layer. In the Sanctuary the most exposed areas tend to face the west and northwest and to bear low shrub. Pidgeon (1938) substantiates this observation with the explanation that strong winds and sun exposure influence the local vegetation type. Each produces a desiccating effect. In the southern hemisphere north-facing slopes are exposed to more sun than those facing south, and in the study area the strong desiccating winds come mainly from the west.

Two other vegetational strata usually occur beneath the *Eucalyptus* canopy. The taller is a shrub layer 10-12 feet high. It is often a discontinuous, patchy layer, of variable density. Some patches in the study area are so dense that they are almost impenetrable by man. The low shrub layer is 5 feet or less in height. On the Sanctuary this layer is more extensive than the tall shrub layer when the upper canopy is tall. It is also highly variable in density. A ground cover of grass is uncommon here. Beneath the shorter stands of *Eucalyptus* a tall shrub layer predominates. Pidgeon (1937) classifies this combination of vegetation types as "low scrub-forest" (pl. 2, b). It predominates on the east-facing slopes of the Sanctuary. On high ridges and west-facing slopes it grades into low-growing shrub.

METHODS

A 22-acre segment of Warrah Sanctuary was selected as the study area. The eastern border of the segment coincided with the eastern border of the Sanctuary, and on this border it was separated from adjoining property by a 10-foot fire-break. A permanent stream flowed through the middle of the segment. Major considerations in the selection of the segment were, first, the inclusion of several types of habitat and, second, the choice of a reasonably accessible area. The fire-break served as a line of north-south orientation and as a suitable place to check the daily catch of animals. The comparatively high trap-yield of small mammals near the stream led to the selection here of a small unit of one-quarter acre which was trapped intensively throughout the study. Trapping in the remainder of the segment was done in small sections, none of which were trapped continually throughout the study.

Trapping was carried on for 145 days and 7,900 trap nights. The area of one-

quarter acre intensively studied was trapped for 96 days for a total of 5,096 trap nights. Live traps of four sizes were employed. Their inside dimensions were (a) $17\frac{1}{2}$ by $8\frac{1}{2}$ by 7 inches, (b) 9 by 3 by $3\frac{1}{2}$ inches, (c) $8\frac{1}{2}$ by 3 by 3 inches, and (d) 8 by $2\frac{1}{2}$ by $2\frac{1}{2}$ inches. The largest trap was made of $2\frac{1}{2}$ by $\frac{1}{2}$ inch wire mesh. The next largest was constructed of sheet metal, and the two smallest were of pressed wood except for a metal trap door. The last two were identical in construction except for size. All traps had an entrance at one end only. Traps of different sizes were set at random in the field; placement was generally not consistent from one time to the next. They were frequently set in pairs or in a line at 40-foot intervals. In the densest portions of the bush, wallaby trails often determined the configuration of the trap line. Only in the quarter-acre unit was a grid pattern practical, and here it was often employed. The bait was a mixture of peanut butter, rolled oats, and honey or raisins. Occasionally sunflower seeds and nesting materials were supplied. All months except January, February, and June are represented in the sample.

The following data were recorded for each animal captured: place of capture and trap number; sex; age estimate; weight; measurements of total length, tail, hind foot, and ear; for males, testicular descent; for females, vaginal perforation and evidence of lactation or pregnancy. Ectoparasites were preserved. Field numbers were assigned and each animal was ear-notched with a number symbol. The animal was released on the same day or on the following day at the point of last capture. Occasionally an animal was kept under observation for several days before release.

RESULTS

Abundance.—In the 22-acre study area, 65 members of *Rattus assimilis* were encountered. Including both initial capture and subsequent recaptures, they were recorded in the traps a total of 182 times—a trap-yield of 2.3 per cent. The large wire trap, in 1,070 trap nights, yielded *R. assimilis* 16 times (1.5 per cent yield). The metal trap, in 1,338 trap nights, yielded 73 times (5.5 per cent). The large wooden trap yielded 85 times in 2,947 trap nights (2.9 per cent). The small wooden trap yielded 8 times in 2,468 trap nights (0.32 per cent). A few miscellaneous traps yielded nothing in 77 trap nights. The foregoing figures indicate that the solid metal trap was the most efficient in the capture of *R. assimilis*. This trap did not swell in heavy rains as did the wooden traps, nor was it easily set off by rain or wind. Trap failure and the subminimal size of the small wood traps undoubtedly account in part for the extremely low average yield of 2.3 per cent. With one exception, only subadults were captured in these small traps. Excluding the small traps and their captures from the count, the trap-night figure is lowered to 5,432 and the total yield is raised to 3.2 per cent. Even this altered figure is very low by usual standards.

The paucity of mammals encountered is still more striking in that, according to trapping results, *Rattus assimilis* appeared to be by far the most common of the small mammals in this area. These results plus field observations strongly suggest that the trapping figures reflect the actual field situation. It is therefore postulated that the population of *R. assimilis* of this area was thin, although not necessarily abnormally sparse for this species in its native habitat. The not uncom-

mon occurrence of *R. assimilis* in very low numbers is further suggested by McDougall (1946b:228): "Although *R. assimilis* has a wide distribution the author has not taken this rat in the Mackay district. It is not concluded that the species does not exist in this district, but rather that, though trapping has been intensive in the correct habitat, years of very low densities have been encountered." In his work with *Clethrionomys*, Evans (1942) suggests that the ultimate survival of a species may depend upon habitats that will maintain only low densities, since high densities permit high predator densities and may lead to the virtual destruction of the prey species. This hypothesis should be considered in view of the low densities of *R. assimilis* which have been reported, although, in the light of conditions in Australia, another hypothesis appears to the author to be more tenable, and is developed later in this monograph.

TABLE 1
DISTANCE BETWEEN POINTS OF RECAPTURE

Distance (in feet)	Recaptures					
	Male		Female		Total	
	N	Per cent	N	Per cent	N	Per cent
0-50.....	24	37.5	37	66.0	61	50.8
51-100.....	4	6.3	7	12.5	11	9.2
101-150.....	5	7.8	2	3.6	7	5.8
151-200.....	12	18.7	6	10.7	18	15.0
201-250.....	5	7.8	1	1.8	6	5.0
251-300.....	4	6.3	2	3.6	6	5.0
Over 300.....	10	15.6	1	1.8	11	9.2

Habitat preference.—The bush rat seems to prefer the stream-border habitat. A certain bias may be present in the data here, since more traps were set near the stream than in any other habitat. In terms of percentage of captures, however, areas more than 100 feet from the stream were only 0.96 per cent effective (5,753 trap nights and 55 captures), whereas the 100-foot band on either side of the stream was 5.9 per cent effective (2,147 trap nights and 127 captures). Distance between points of recapture indicates a modal wandering of 50 feet or less for both sexes (table 1); so a stream habitat seems to influence the local numerical distribution of this rodent.

The foregoing does not imply that ready access to water is necessarily important. *Rattus assimilis* is a ground dweller, and according to Brazenor (1936) it makes burrows beneath fallen logs, at the base of thick vegetation or beneath its overhang. "As a rule the burrows are not deep; they slope gently down to an enlarged chamber in which is a nest of grass.... This rat leaves no noticeable tracks, for its runs seldom extend far from the mouth of its burrow and have not a well-used appearance" (*ibid.*:67). The advantages of the stream border to a ground-dwelling rat are the abundance of fallen logs resulting from rapid stream erosion after heavy rainfall, and the moist and friable soil in which to form bur-

rows and establish a nest. In Warrah Sanctuary, an area of sandy, hard, and shallow soil, a stream habitat offering favorable cover for burrow systems seems to be of prime importance to this species.

McDougall (1944b) states that the northern race *Rattus assimilis coracius* is confined to rainforest ("scrub") and adjoining localities. If cane fields are adjacent to rainforest, this rodent will invade the cane, but "compared with the populations of other rats in cane, it is encountered in small numbers only and seldom more than 50 yards from its native habitat" (*ibid.*:42). Although this rat will eat cane, it occurs in such small numbers in the fields that McDougall does not consider it an economic threat to the harvest. The important point here is that its optimal habitat is rainforest, which seemingly offers the most suitable burrowing conditions for a ground-dwelling rodent that is structurally nonfossorial. McDougall (1946b:162), once had a 50 per cent yield in virgin rainforest at Abergowrie, Herbert River district, the only area in which he found a concentrated population of the species.

Populations of *Rattus assimilis assimilis* have been recorded several times in pine plantations—an exotic habitat totally unlike anything offered by native Australian plants. Extensive plantings of pine (mostly *Pinus radiata*) have been made throughout eastern Australia in plots surrounded by native bush. Bracken is a common undercover in these plantations. Invasions of *assimilis* from the bush into the pine plantations in south Queensland and in Victoria (McNally, 1955) have resulted in extensive damage to trees. This rodent causes severe damage by ringbarking the trees. In such forested areas *assimilis* has been encountered recently in abundance (McNally, 1955, and *in litt.*), and McDougall (1946b) records visitations (= outbreaks?) of this species in forestry projects from 1932 to 1934. To date these visitations have not been recognized as cyclic in nature. Here again the habitat, although artificial and simple in floral content, is especially suitable for this rodent. When the ground is carpeted with pine needles and bracken, the surface becomes readily workable for a ground inhabitator like *assimilis*. McNally (1955) has found their burrows under rotted stumps and their runs in the underbrush. He feels that removal of this cover would eliminate the rats.

The author does not mean to emphasize unduly the importance of suitable burrowing habitat and its relation to the over-all distribution of *Rattus assimilis*. As in any species of mammal, a combination of factors governs the extent of its distribution. It is suggested here, however, that opportunity to establish burrow systems may have a very significant bearing on the local numerical distribution of this rodent.

EARLY DEVELOPMENT OF THE YOUNG

Field study of the reproductive biology of an animal is greatly facilitated by the establishment of a series of age groups. A basis for making age determinations in the field and for calculating an approximate growth curve was established by following the early development of a field-bred, laboratory-raised litter. A pregnant female was held in the laboratory and five days later gave birth to a litter of three. Weights and measurements of this litter are recorded in table 2 and figures 2, 3, and 4.

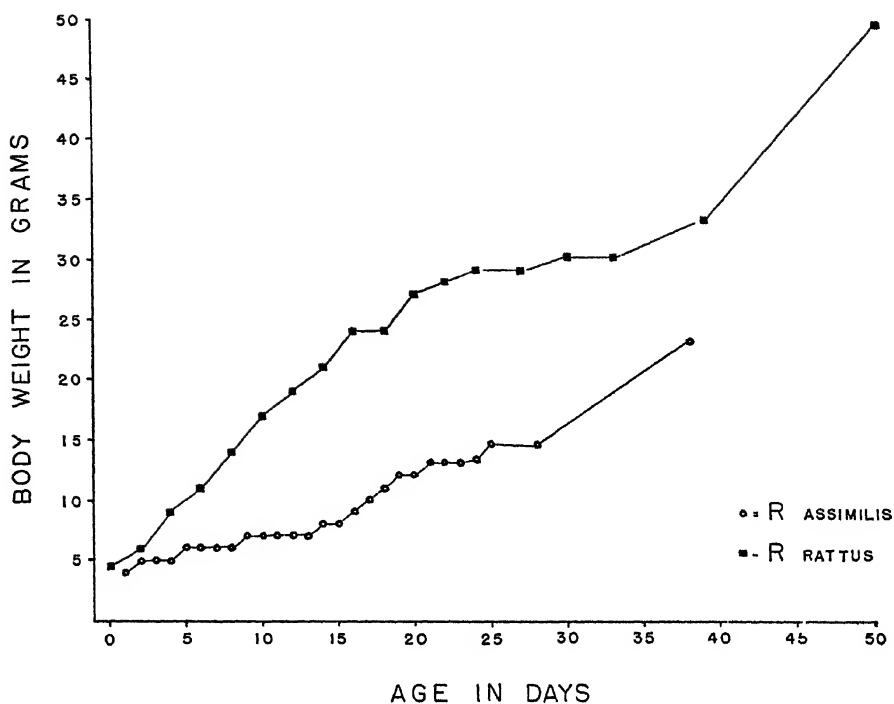


Fig. 2. Body weights of a field-bred, laboratory raised litter of *Rattus assimilis* and of a litter of *Rattus rattus*.

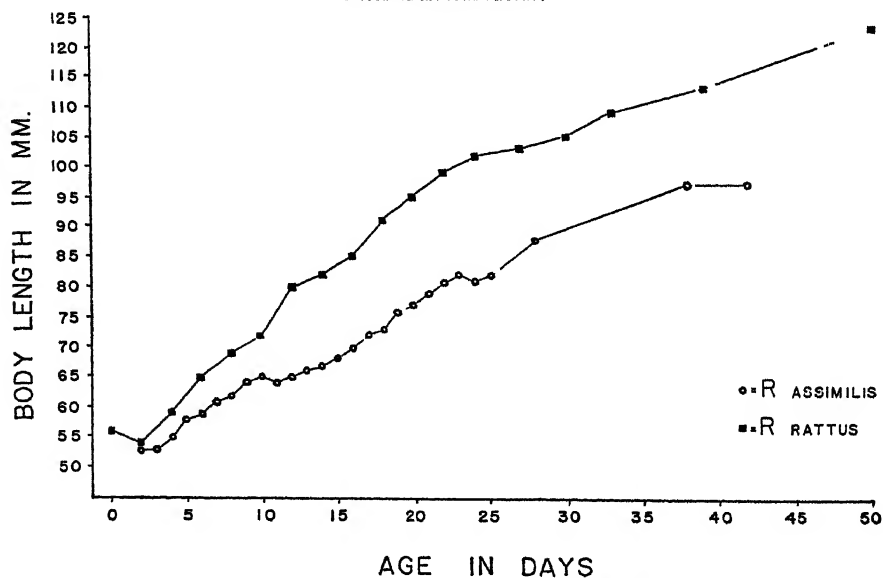


Fig. 3. Body lengths of a field-bred, laboratory-raised litter of *Rattus assimilis* and of a litter of *Rattus rattus*.

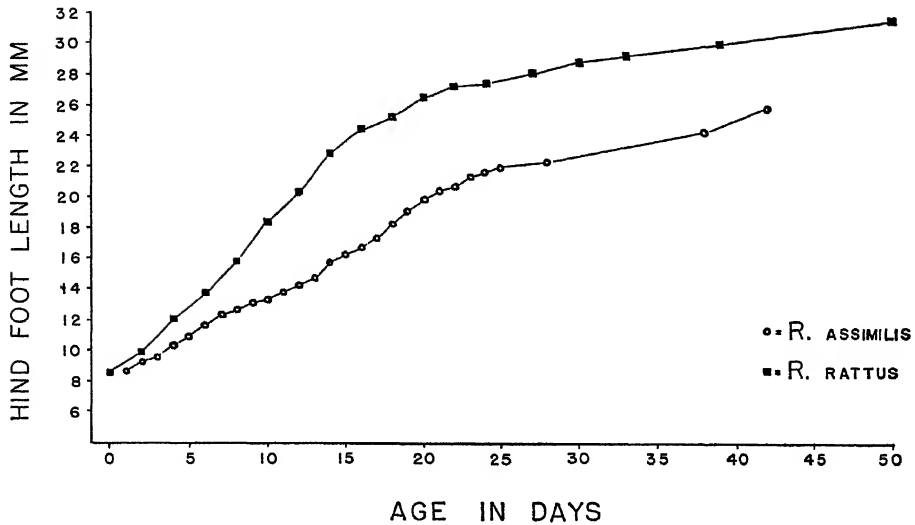


Fig. 4. Hind-foot lengths of a field-bred, laboratory-raised litter of *Rattus assimilis* and of a litter of *Rattus rattus*.

Day 1 (24–48 hours after birth): The young were pink and hairless except for small unpigmented mystacial vibrissae. Eye pigment was apparent through the closed lids, and eye slits were visible as slightly pigmented lines. Ear pinnae were closed, and the umbilical scar was prominent. Milk was clearly visible in the stomach. Males could be distinguished from females at this stage by the greater distance from anus to urogenital aperture (average distance 2.6 mm. for male, 1.7 mm. for female).

Day 2: Skin color was still pink but slightly darker everywhere except for feet and tail. One long vibrissa (interramal) measuring 4.9 mm. in length, extended from lower lip in midline region. The shorter mystacial vibrissae were apparent as a slight fuzz, and very short superciliary vibrissae were present. The scrotal region of the male was slightly pigmented, but the female urogenital area contained no pigment. No sign of mammary glands was apparent on the female. Ear pinnae were still folded and the umbilical mark was conspicuous. Teeth were not apparent, nor could they be felt. Palmar and plantar tubercles of the feet were prominent.

Day 3: Skin was darker and more wrinkled. Ear pinnae were beginning to unfold or were free. There were several conspicuous submental vibrissae. No teats were apparent, but the umbilical mark was distinct. No teeth had erupted.

Day 4: The young were darker dorsally and had acquired a very short fine covering of body hair. Ear pinnae were free, although ear openings were still closed. The umbilical scar was still evident. No teats were apparent and the teeth could not be felt.

Day 5: The dorsum was more heavily pigmented. Slight pigmentation was apparent on the distal portion of the pinnae. The skin of the venter was more opaque,

for the milk-filled stomach was barely distinguishable. Ears and eyes were closed. The umbilical scar was present, but there was no sign of teats.

Day 6: The distal portion of each pinna showed distinct pigmentation. Conspicuous swelling in the muzzle region at the location of the mystacial vibrissae gave the animal a broad-snouted appearance.

Day 7: Tail and legs, from upper arm and upper leg, were still pink throughout

TABLE 2
GROWTH OF A FIELD-BRED LITTER OF *RATTUS ASSIMILIS ASSIMILIS*

Days old	Weight (grams)		Hind-foot length (mm.)		Body length (mm.)	
	Range	Average	Range	Average	Range	Average
1.....	4	4	8.5-8.8	8.6	55-59	56
2.....	5	5	8.9-9.3	9.2	50-55	53
3.....	5	5	9.5-9.6	9.5	52-56	53
4.....	5	5	10.3	54-56	55
5.....	6	6	10.8-11.0	10.9	57-59	58
6.....	6	6	11.5-11.8	11.6	58-60	59
7.....	6	6	12.2-12.3	12.3	60-63	61
8.....	6	6	12.7-12.8	12.7	60-65	62
9.....	7	7	13.0-13.1	13.1	62-65	64
10.....	7	7	13.2-13.5	13.3	64-66	65
11.....	7	7	13.7-13.9	13.8	63-66	64
12.....	7	7	14.2-14.3	14.2	64-66	65
13.....	7	7	14.5-15.0	14.7	64-68	66
14.....	8	8	15.5-16.0	15.7	67-68	67
15.....	8	8	16.0-16.5	16.3	68-69	68
16.....	9	9	16.6-16.9	16.8	69-71	70
17.....	10	10	17.2-17.6	17.4	70-73	72
18.....	11	11	18.2-18.4	18.3	73-74	73
19.....	12	12	19.0-19.3	19.1	75-77	76
20.....	12	12	19.6-20.4	19.9	77	77
21.....	13	13	20.1-20.8	20.5	79	79
22.....	13	13	20.7-20.9	20.8	80-81	81
23.....	13	13	20.9-21.8	21.4	81-82	82
24.....	13-14	13.3	21.1-22.1	21.7	80-81	81
25.....	14	14	21.9-22.3	22.0	82	82
28.....	14	14	22.1-23.0	22.4	87-88	88
38.....	..	23	24.5	97
42.....	20-24.5	22.5	26	26	95-98	97

their length, but the heel of the hind foot and the dorsal aspect of the tail were beginning to acquire pigmentation. Superciliary papillae and vibrissae were apparent for the first time. The umbilical scar was evident, but there was still no sign of teats.

Day 8: Pigment had extended over the entire dorsum of the head and to posterior and lateral aspects of the hind legs, and there was a slight indication of pigment on the anterior surface of the wrist region. Hair tracts were distinctly visible. The longest facial vibrissae were unpigmented and measured 10 mm. long.

In addition to righting movements, which were evident from Day 1 on, crawling motions were first observed.

Day 9: The young rats were assuming a soft slate-gray texture dorsally, rather than the previous dry wrinkled appearance, and body hair had erupted to a length of about 1 mm. Teats were readily discernible on the female. The umbilical scar was still apparent. Incisors had not erupted, although both upper and lower incisors were visible through the gums. The clitoris of the female was only slightly shorter than the penis of the male, and both structures were much larger and more protruding than the dark scrotal area of the male.

Day 10: Eyes and ears were still closed. Genal and interramal vibrissae were now distinct. The umbilical scar was no longer discernible. Incisor teeth had not erupted but were conspicuous beneath the gums.

Day 11: The dark head and shoulder region was tinged with brown middorsally, and the sides of the body were brown, leaving only the posterior middorsal region slate-colored and the venter unpigmented. Teeth had not erupted and ears and eyes were still closed.

Day 12: The body hair covered the venter as well as the dorsum, giving the entire animal a furry appearance. The pattern of black and brown hairs gave a penciled effect to the dorsal pelage. Silvery hair on the upper surfaces of the feet, a trait retained throughout life, was now evident. Upper incisors had erupted, but the lowers had not penetrated the gums. The tail was finely covered by very short unpigmented hairs. The scrotal sac was now heavily pigmented.

Day 13: Eyes and ears were still closed. Lower incisors were erupting, but in most instances had not pierced the gums completely.

Day 14: The brown pigment of the body fur had extended posterodorsally; only the midrump region was slate-colored. The muzzle had darkened, and a short (one-eighth inch) but conspicuous dark line ran obliquely posterodorsally from the anterior end of the eye slit. Ear pinnae were pigmented except at the base. All incisors had erupted. Eyes and ears were still closed. For the first time the beginning of body temperature control was noticeable. The young rats retained a detectable degree of warmth during the time of observation, and made successful attempts to establish contact with each other while on the measurement table.

Day 15: The darkened muzzle and "superciliary stripe" were less distinct. Eyes and ears were still closed. Movements showed greater coördination, and the legs were pulled in under the body when the animals were at rest. Previously the legs had been splayed out to either side with the entire venter touching the substratum. Unsteady walking with the legs beneath the body and the raising of the body off the ground were first observed, as were washing and scratching movements.

Day 16: Ear pinnae were finely furred to the extremities. Eyes and ears were closed. Facial vibrissae were unpigmented and measured up to 17 mm. in length. The rats walked about more, although unsteadily.

Day 17: Eyes and ears were still closed. Body hairs of the venter were white-tipped and light gray at the base. A white pectoral spot in which the hairs are white from base to tip is not common in this subspecies; when it occurs it could be discerned at this age. In the northern subspecies, *Rattus assimilis coracius*, this pectoral spot is much more common.

Day 18: Eyes and ears had not opened.

Day 19: Eyes and ears were still closed, but ears were almost perforate.

Day 20: One or both eyes were open, and ears had opened. Facial vibrissae ranged up to 24 mm. in length, and a pigmented base was discernible on some. Coördination was markedly improved. The rats were able to rest on their hind legs and wash their heads with both forefeet. They walked actively and appeared to be aware of heights, for they would stop suddenly at the table edge.

Day 21: Eyes were completely open. The scrotal region of the male was relatively inconspicuous except for dark pigmentation. The rats ran about continuously and were able to climb out of the shallow weighing pan. Face washing was a frequent activity.

Day 22: Pelage was by now very dense and soft. Dorsal hair length averaged 7 mm. The animals were exceedingly active while being measured, and rapidly recovered from slipping or falling.

Day 25: Successful attempts at eating solid food (apple) were first noticed on this day. The ventral fur was by now soft and dense.

Day 28: Ventral hair covered the anal region, which could not be seen without first brushing aside the fur surrounding it. The vagina was closed.

Day 38: Dorsal hair length averaged 10.5 mm., of which the basal 8 mm. was slate gray and the distal tip was brown. The longest mystacial vibrissa was 40 mm. long, the basal half of which was black and the distal portion white. The vagina was closed.

Day 41: Dorsal hair length was the same as on Day 38. Along the dorsal and lateral portions of the body a new brown-tipped coat, the future adult pelage, was evident and measured 1 mm. or less in length. The longest mystacial vibrissa was 44 mm. long. The vagina was perforate. Testes were abdominal in position.

AGE AND GROWTH

The division of a population into a series of age groups is important to the understanding of the reproductive biology of the animal in the field. One of the most obvious aids in determining age is weight, which can be obtained with ease, rapidity, and accuracy. In rodents, at least, weight is a more accurate indicator during the first month than it is later. The length of the hind foot is perhaps a better age indicator from then on to the adult level, but it is difficult to measure it accurately from a living animal.

Using a scale of weights and measurements of a litter of known age, older age categories can be approximated with this scale as a base point. A combination of weight and hind-foot length is used to place field-caught individuals in one of three categories: juvenile (weight 30 grams or less, hind-foot length 27 mm. or less), subadult (weight over 30 grams and less than 50 grams, hind-foot length over 27 mm. and less than 31.5 mm.), and adult (weight 50–180 grams, hind-foot length over 31 mm.).

These three categories, although arbitrarily defined by weight and measurement, were established to reflect in a very general way the reproductive status of the animal. The juvenile category is limited to rats less than 1½ months old, and members of this age group show no evidence of reproductive activity. The

testes are abdominal in position and the vagina is closed or recently perforate. The juvenile pelage is grayer than the adult pelage and lacks long guard hairs. The erupting adult pelage may be seen in older individuals of this category upon parting the juvenile coat. The subadult category is difficult to define except by measurement. It covers the age period from about $1\frac{1}{2}$ to 3 months. The animals are reaching sexual maturity at this time. The vagina is commonly perforate, and the testes are abdominal or descending into the scrotal region. There is no field evidence in the present study of breeding in this category. In the smaller individuals of this group the adult pelage is replacing the juvenile hair and molt lines are conspicuous. The adult category is set up to include individuals over 3 months of age. Early in the adult stage there appears to be considerable gain in weight, although linear gain is minimal. Increase in hind-foot length is ordinarily not more than 3 mm. The testes are large and usually scrotal in position, and lactation or pregnancy is common.

Linear growth and weight increment can be influenced appreciably by conditions during captivity. Leslie *et al.* (1952) demonstrated that in field-caught and laboratory-raised *Rattus norvegicus* of comparable age the laboratory-raised animals may weigh considerably less. The balance may also tilt in the other direction, as will be seen in the laboratory study of *R. assimilis*. Post-weaning age determinations are therefore estimated entirely from data from field-caught specimens in the present study.

These three age categories, as recognized in the rat population in the field, are established and described from the examination of 61 field-caught individuals. Figure 5 shows the relation between weight and hind-foot length and the amount of variation. The range of ages within the categories is based on the capture of two very young rats that were subsequently recaptured more than once over a period of several months. Their ages were approximated from the growth curve of the litter born and raised in captivity (fig. 6). In dealing with these categories two assumptions must be made: (a) that there is essentially no seasonal variation in growth rates and (b) that a normal rate of growth is demonstrated by the two individuals used as the basis for the given age assignments. The first assumption is based on the fact that none of the data now available, admittedly few though they are, indicate seasonal variation in the growth rates of any of the Australian rodents. Harrison (1956) found no seasonal variation whatsoever in Malayan rodents, where, of course, the climate is very constant. The second assumption is based on the low proportion of recaptures encountered in the present study. The ages assigned to the categories are necessarily approximate. There may be a disparity between the growth rates of males and of females, as Harrison (1951) found in members of the subgenus *Rattus*, but at present no distinction can be made from these field data.

The youngest specimen of *R. assimilis* captured was estimated to be $3\frac{1}{2}$ weeks old (weight 13 grams, hind-foot length 22.2 mm.) by use of figure 6, and is thus assigned to the juvenile category. The eyes had been open for about four days; judging again from the laboratory-raised litter, this is the age at which solid food is first consumed. Whether or not the maternal nest was still being occupied by this young field-caught individual, its capture in a trap suggests that it was

foraging on its own and that weaning was occurring, or had occurred, at this time.

On November 29, 1954, a juvenile weighing 25 grams and measuring 27 mm. in hind-foot length was captured and subsequently released. On April 3, 1955, the animal, now an adult, weighed 83 grams and the hind foot was 33.0 mm. long. In 18 weeks its weight had increased by 232 per cent and the hind-foot length by 22 per cent. The average growth rate per week over this period is 3.22 grams and 0.33 mm. in hind-foot length. On July 25, 1955, the animal weighed 121 grams

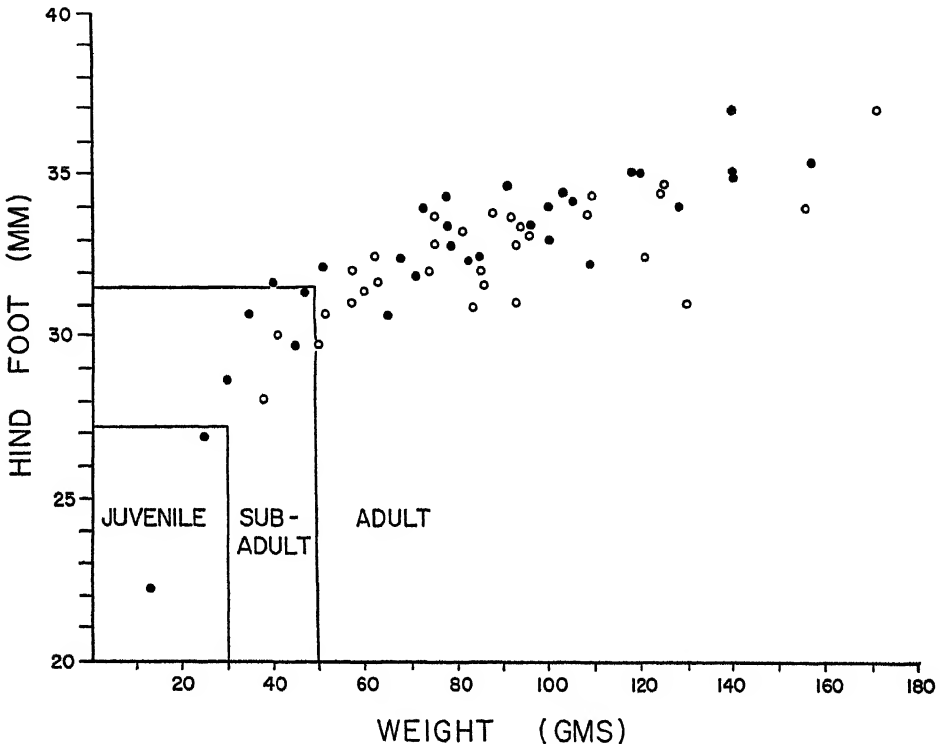


Fig. 5. Age categories of *Rattus assamensis* in the field. The open circles represent females; the solid circles, males.

and the hind-foot length was 34.4 mm. This represents a 45.8 per cent increase in weight and a 4.2 per cent increment in hind-foot length from the time of previous capture. Over this 16-week period the rat had increased in weight at the average rate of 2.3 grams per week and 0.09 mm. in hind-foot length per week.

A young rat when first captured on May 6, 1955, weighed 30 grams and the hind foot measured 28.8 mm. When captured 11 weeks later, on July 24, 1955, it weighed 89 grams and the hind foot measured 34.0 mm. This animal had increased in weight by 200 per cent and in hind-foot length by 18 per cent. The increment is at the average rate per week of 5.4 grams in weight and 0.47 mm. in hind-foot length. By very definition, "average growth rate" may never represent the actual rate of growth at any given time; but since rats are said to grow "fairly continuously and evenly, up to a certain size" (Harrison, 1956:7), these

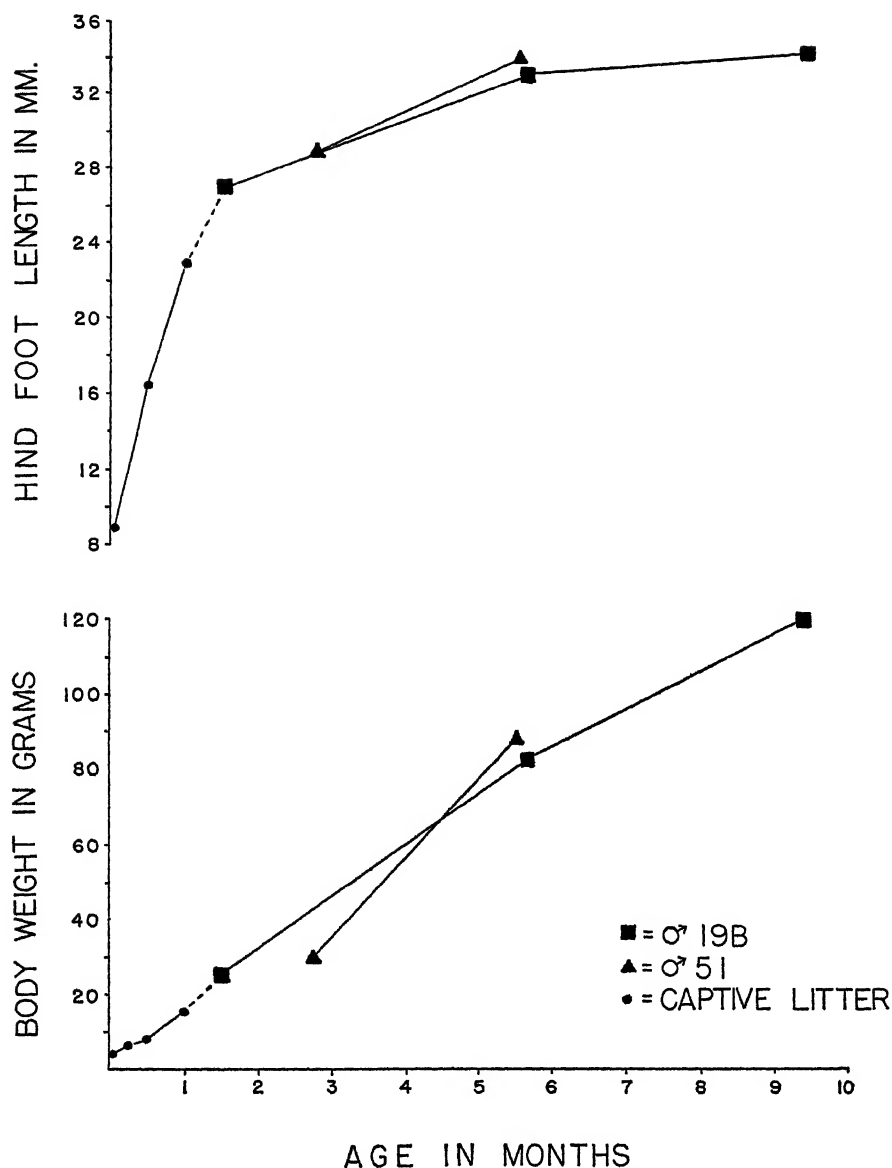


Fig. 6. Growth-curve approximation of *Rattus assimilis* in the field.

figures give some idea of the degree of increase per given time unit from juvenile to young adult under field conditions.

Minor weight fluctuations among fully adult rats, that is, those in which linear growth has virtually stopped, are common under field conditions. These fluctuations seem to depend mainly on daily intake of food and on pregnancy. Minor variations of less than 10 grams may be attributed to daily food intake. Parasites evidently play a very subordinate role, if any, in the weight fluctuations of healthy

individuals. The adults seem to reach individual weight equilibria from which they vary only slightly. Adults recaptured after an interval of two or three months usually weighed within 10 grams of their previous weight. Parturition accounted for one drop in weight of 16 grams.

It is difficult to reconcile the trend of minor individual weight fluctuations with the enormous disparity in the adult weights of various individuals. Adult weights

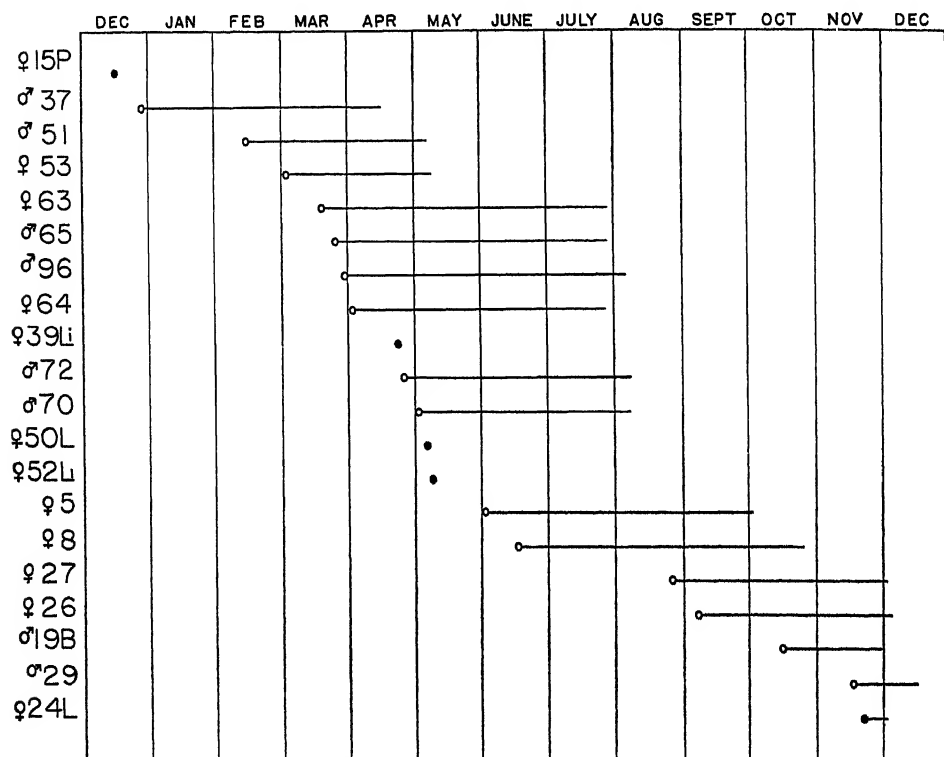


Fig. 7. Evidences of breeding in the field. The open circles represent approximate time at which young were born, estimated from juvenile and subadult captures; length of horizontal line connecting with circle represents age estimate at time of capture. The solid circles are estimates from pregnant (P) or lactating (L) females, or are recorded births (Li).

of essentially nongrowing individuals varied from 105 grams to 171 grams. Males tended to be heavier than females; the heaviest female weighed 157 grams. Since weight becomes a progressively less satisfactory age determiner from weaning to adulthood, and since fully adult animals tend to exhibit only minor variations, increase in weight is apparently most variable during the subadult and early adult periods. Although sex differences may account for part of the disparity, the differential rate of weight increase in subadult and early adult stages, regardless of the sex of the animal, is important also and may actually reflect the relative nutritional intake of individuals at that time. Such modification in nutritional intake may be a function of local habitat differences or of seasonal changes in the vegetation.

BREEDING

Information as to when litters are born in the field is obtained from the capture of juveniles, subadults, and pregnant and lactating females. Age has been calculated for 15 young field captures. The maximum error in the age determination of these specimens is estimated to be less than three weeks. The results, tabulated in figure 7, indicate that litters were produced during every month of

TABLE 3
MUSEUM SPECIMENS OF *RATTUS ASSIMILIS ASSIMILIS*

AUSTRALIAN MUSEUM			
♂ M1367.....	Burraborang Valley, N.S.W....	Oct. 1898	subadult
♂ M3843.....	Cutter's Pass, William's River, N.S.W.....	Oct. 1926	subadult
♂ M5109.....	Wahroonga, N.S.W.....	March 1931	subadult
♀ M5525.....	Coolong, N.S.W.....	April 1934	subadult
♂ M6737.....	Gympie, Qld.....	May 1940	subadult
♂ M6875.....	Mt. Irvine, Bell, N.S.W....	Nov. 1943	subadult
♀ M6876.....	Mt. Irvine, Bell, N.S.W....	Nov. 1943	subadult
♂ M6900.....	Mt. Irvine, Bell, N.S.W....	May 1944	subadult
NATIONAL MUSEUM OF VICTORIA			
♀ C1396.....	Wingan Inlet, Vict.....	Feb. 24, 1946	subadult
♀ R12982.....	Mansfield, Vict.....	Jan 14, 1932	subadult
♀ R12980.....	Mansfield, Vict.....	Jan. 14, 1932	subadult
♀ R12974.....	Mansfield, Vict.....	Jan. 14, 1932	adult, 3 embryos
BRITISH MUSEUM			
♂ 25.8.1.14.....	Guy Fawkes Dist., N.S.W....	April 5, 1924	immature
♀ 26.3.11.161.....	Guy Fawkes Dist., N.S.W....	April 17, 1924	immature
AMERICAN MUSEUM OF NATURAL HISTORY			
♀ 65878.....	Glen Ferneigh, N.S.W.....	Sept. 27, 1921	subadult

the year except January and July. Brazenor, however, collected a female with three embryos on January 14, 1932, near Mansfield, Victoria (National Museum of Victoria, ♀ R 12974). In the museum collections examined juveniles and subadults are represented in all months of the year except June, July, August, and December (table 3).

Breeding is then essentially nonseasonal, although there may be seasonal fluctuations in the amount of breeding activity in the course of a year. As many young are born in March, April, and May as are recorded in all other months put together (fig. 7), but whether this peak is real or circumstantial cannot be determined without more data. At Pearl Beach the highest rainfall, however, coincides

with this three-month period. Harrison (1952:129) states that in Malayan rodents "there is a tendency for an increase of rainfall to be accompanied by an increase of pregnancy rate and *vice versa*."

The evidence for year-round breeding in *Rattus assimilis* becomes increasingly interesting in view of the fact that most of the native mammalian co-inhabitants of the area show a marked breeding season. The spiny anteater, *Tachyglossus aculeatus*, breeds once a year in winter or early spring, from June to September (Flynn and Hill, 1939). The yellow-footed marsupial mouse, *Antechinus flavipes*, appears to breed only in late winter or early spring (Horner and Taylor, 1959). The brushtail possum, *Trichosurus vulpecula*, has two breeding seasons per year spaced about six months apart (Bolliger and Carrodus, 1939). The sugar glider, *Petaurus breviceps*, breeds once a year (Troughton, 1954) and so does the ringtail possum, *Pseudocheirus laniginosus* (*ibid.*). The long-nosed bandicoot, *Perameles nasuta*, however, breeds in every season with a suggestion of two peaks in the year (Lyne, *in litt.*). The breeding season of the black-tailed wallaby, *Wallabia bicolor*, is unknown. (A 22-gram pouch young of this wallaby was recorded from near Pearl Beach on December 22, 1954.) Besides *Rattus assimilis*, the other endemic murid rodent present, *Hydromys chrysogaster*, breeds only once a year (Troughton, 1954). The introduced murids *Rattus rattus* and *Mus musculus* probably breed throughout the year.

In the Malayan climate, which is more uniform throughout the year than that of New South Wales, Harrison (1956) finds that there is no restricted breeding season in the endemic *Rattus*, although certain fluctuations in breeding activity may be correlated with rainfall. Davis (1953:380) states that "rats, unlike most rodents, are able to reproduce in nature at all seasons of the year."

In the Australian situation it is interesting to speculate whether the continuous breeding activity of *Rattus assimilis* may not represent a genetic "relict" of their east Asian ancestry which the seasonal variations of this more southern climate have yet to "modify." It seems likely, however, that breeding is continuous only for a given population as a whole; for individuals within a population, breeding periods followed by intervals of nonbreeding probably recur throughout the year. Since the periods are not in synchrony, there can be continuous production of a small number of young the year around, which may be of great selective value in the perpetuation of the species at a low density level.

Litter size.—Some members of the genus *Rattus* have exceedingly large litters: those of *R. norvegicus* and *R. (Mastomys) coucha* commonly consist of 12–15 young. A few data were obtained on litter size of wild *R. a. assimilis*. Two field-caught females bore litters of 3 each in the laboratory. A pregnant female that died in a trap carried 6 embryos, 4 in the left uterine horn and 2 in the right. One museum specimen (National Museum of Victoria, ♀ R12974) contained 3 embryos.

Litter size in the field-caught Australian *Rattus conatus* varied from 3 to 7, with a mean of 6 (McDougall, 1946a). In the eight species of Malayan *Rattus* studied by Harrison (1955), the mean number of embryos per litter ranged from 3.0 to 4.3.

Sex ratio.—The sex ratio of individuals of *Rattus assimilis* captured over the

year was 34 males to 31 females. When an entire population of *R. conatus* was taken from an area, McDougall (1946a:40) found that trapped specimens included an equal number of males and females, and Harrison (1955) found a 50:50 sex ratio in most of the Malayan members of *Rattus*.

LONGEVITY

In his work with *Rattus conatus* of Queensland, McDougall (1946a:11) states that "due to survival and movement of populations, a period of 101 days is the maximum which can be expected for studying any particular rat in the field." Of the *R. assimilis* encountered in the present study, 50 per cent were captured only once. These were juveniles and subadults as well as adult specimens. The longest period over which a rat was followed in the field was 251 days. Three other individuals were followed for 100 days, three for 90 days, and the mean duration for the rest was 19.4 days. The last figure is partly influenced by the fact that 16.5 per cent of the rats died either in the trap or during the brief stay in the laboratory. McDougall (1946b) suggests that "shock disease" (Green and Larson, 1938) may account in part for deaths of Australian ground rats during trapping or handling. Whatever the cause may be, it was obvious in the present study that *R. assimilis* was not as hardy to sudden environmental changes as was its relative *R. rattus*.

Since the recapture data indicate movements of only a few hundred feet among rats encountered several times in the field (table 1), it seems likely that some of the rats were temporary or permanent residents in the area and others were transients. Both groups include young and adult animals. The sudden capture of fully adult unmarked specimens in an area which has been trapped extensively for several months points to the existence of transients.

Extrapolating from the data on growth rates of subadults and young adults, it seems reasonable to conclude that the weight of 100 grams is usually attained by the seventh month if not before. Of the 46 adults encountered, 20 weighed more than 100 grams, which suggests that almost half of the adults were over seven months old. Therefore the normal life expectancy for those *Rattus assimilis* which reach maturity in the field is estimated not to exceed a year. Otherwise we should expect a much higher percentage of adults in the category of those weighing more than 100 grams. Mack (*in litt.*) supports this statement; his impression is that the native *Rattus* of Australia have a very short life span, perhaps up to a year.

COMPARISON WITH *RATTUS RATTUS*

The introduced roof rat, *Rattus rattus*, is distributed throughout most of Australia and, in addition to inhabiting areas of human civilization, it is reported to live and breed in the native bush. This rat occurred in and about buildings near the Warrah Sanctuary, on cultivated land, and on the marginal areas of the Sanctuary itself. During the present study, 19 individuals were captured, 13 of them near buildings or on cleared land, and 6 on the Sanctuary. At no time was *R. assimilis* ever found near human habitation or on cleared land along with the *R. rattus*. Four specimens of *R. rattus*, in turn, were trapped on the Sanctuary less than 50 feet from the firebreak adjacent to cultivated land, and two were

trapped in the native bush 225 feet from the firebreak. The overlap in occupied area between the two species of *Rattus* seems, therefore, to be fairly restricted.

Although destruction of habitat is said to be a main factor contributing to the depletion of the native murine fauna, Brazenor (1936) and others express the view that an equally important factor is the actual expulsion of all the native rats and their gradual replacement by the introduced *Rattus* until the native species are extinct. The present author believes that disturbance of the native bush is the primary factor in the depletion of *R. assimilis*, whether or not the area

TABLE 4
GROWTH OF A FIELD-BRED LITTER OF *RATTUS RATTUS*

Days old	Weight (grams)		Hind-foot length (mm)		Body length (mm)	
	Range	Average	Range	Average	Range	Average
0	4-5	4.5	8.3-8.7	8.5	53-59	56
2		6		9.7		54
4	8-10	9	12.0	12.0	59	59
6	11-12	11	13.7	13.7	65	65
8	13-15	14	15.6-16.3	15.8	68-70	69
10	17-18	17	18.0-18.8	18.4	70-76	72
12	19	19	19.6-21.0	20.3	79-81	80
14	20-22	21	22.8-23.2	22.9	79-84	82
16	23-24	24	24.0-24.8	24.5	83-90	85
18	24-25	24	25.0-25.6	25.3	90-93	91
20	27-28	27	26.1-26.8	26.6	93-97	95
22	28-29	28	27.0-27.8	27.3	96-101	99
24	28-29	29	27.0-27.9	27.5	100-105	102
27	28-29	29	27.9-28.4	28.2	101-105	103
30	29-30	30	28.5-29.7	29.0	101-107	105
33	29-31	30	29.4-29.8	29.5	108-111	109
39	31-35	33	29.8-30.8	30.2	109-118	113
50	44-56	49	30.1-33.4	31.8	120-127	123

is then invaded by *R. rattus*. If the bush is subsequently invaded, the presence there of *R. rattus* may perhaps accelerate this depletion; but in the area examined the "buffer strip" between cleared land and *R. rattus* versus undisturbed native bush and *R. assimilis* was a narrow one and appeared to be at equilibrium throughout the year.

The early developmental period of *Rattus rattus* is shown in table 4 and figures 2, 3, and 4. It represents weight, body length, and hind-foot length of a field-bred litter of four which was born and raised in captivity under conditions similar to those of the litter of *R. assimilis*. On Day 1 the weights of the two species were about the same, but by Day 20 *rattus* weighed 133 per cent more than *assimilis* of comparable age, and hind-foot measurement of *rattus* was 34 per cent greater. As adults, however, the two species in this locality had about the same range of weight: for adult female *rattus* it ranged from 85 grams to 156 grams; for adult male *rattus*, from 99 grams to 201 grams. The hind foot tended to be a little longer

in adult *rattus*. The pinnae began to open on Day 2 (Day 3 for *assimilis*), incisors erupted on Day 10 (Day 13 for *assimilis*), ears opened on Day 12 (Day 20 for *assimilis*), eyes opened on Day 14 (Day 20 for *assimilis*), and solid food was first taken on Day 18 (Day 25 for *assimilis*). Under comparable conditions the rate of growth and development in the pre-weaning stage is therefore considerably faster in *R. rattus* than in *R. assimilis*.

Judging from the pre-weaning growth curves of the two species, *Rattus assimilis* seems to be less reproductively efficient than *R. rattus* of the same area. It takes longer for *R. assimilis* to "launch" a litter, thus prolonging the length of time a helpless litter is subject to predation. (A large monitor lizard, *Varanus varius*, caught on December 25, 1954, regurgitated seven rats less than two weeks old.) Judging also from these data on growth and development, *R. rattus* probably becomes sexually mature sooner than *R. assimilis*, and, because of the shorter period of lactation, a female *rattus* can probably produce more litters in a given time than can *assimilis*.

The author postulates, however, that a higher reproductive output would not necessarily be an advantage to *Rattus assimilis*. In a marginal habitat of low productivity, maximum exploitation on a long-term basis may best be achieved by maintaining a fairly constant low population level. On the sandstone soils of Australia "there are no native annual species [of plants] . . . because the nutrient levels of the soils are so low that an annual plant cannot obtain sufficient nutrients in a small period of time to survive from year to year" (Beadle, 1953:428). In a stable and nutritionally deficient habitat, of which Warrah Sanctuary is an example, the low density level of the rats, made possible by a relatively low reproductive rate and by the spreading of the reproductive effort over the entire year, may be of long-term selective advantage to these murids.

REPRODUCTIVE BIOLOGY IN THE LABORATORY

A study of the reproductive biology of *Rattus assimilis assimilis* under laboratory conditions was begun from a nucleus of 31 rats live-trapped from the study area at Pearl Beach in August, 1955. They were sent by air to the United States at the end of that month; 8 died en route or within two weeks after arrival. Two months after shipment from Australia, however, the colony of rats began to produce offspring and continued to do so for the subsequent 30-month period. This record of the breeding of *R. a. assimilis* in captivity and a brief description of its housing and food requirements have already been published (Horner and Taylor, 1958). There appears to be no record in the literature of any previous attempt to breed this species in captivity.

The 23 rats which survived the initial period of captivity in the United States were subsequently divided into two colonies: the larger (5 females and 12 males) gave rise to the breeding stock which provided the main source of data for the present study. The other colony (Smith College colony) was used for behavioral and anatomical studies by another investigator. Some of the data derived from the two colonies were exchanged; references to the Smith College colony, when used in the present study, are so designated.

MATERIALS AND METHODS

The larger colony, housed at the University of California, was set up to obtain the greatest amount of breeding activity. Except during pregnancy and lactation, the colony was paired to the maximum. A complete life history was kept of every individual, and the rats were distinguished by the same ear-notching technique which had been employed in the field. Sibling and parent-offspring matings were avoided except on rare occasions.

A catalogue card recording parentage, date of birth, weight and linear growth, matings, and date of death was kept for each animal. Upon the death of a male, an autopsy was performed in order to record the position and weight of the testes, weight of the epididymides and seminal vesicles, and to preserve the testes and baculum; a gross examination of other organs was made. For a female, the mammary formula and the location of the teats, the condition of the mammary glands, the presence or absence of vaginal perforation, and the number, position, and size of embryos were recorded; also included were the examination and preservation of ovaries and uteri, and a gross examination of other internal organs. Total weight, total length, and measurements of tail, hind foot (including claw), and ear (from notch) were recorded for both sexes, and the adrenals were preserved. A museum skin and skeleton were prepared from every usable specimen.

The gonads of both sexes were preserved in Bouin's fixative. After 12-24 hours of preservation the testes were cut into quarter-inch slices to allow maximum penetration of the fluid. A small piece of testis was sectioned and each complete ovary was sectioned serially. All sections were cut at 10-20 microns and stained with Delafield's hematoxylin and eosin. To test for male fertility, biopsies were occasionally performed by cutting out a small section of epididymis and preparing a slide smear. Presence of sperm was determined directly from microscopic examination of a wet preparation or the smear was permanently prepared by allowing it to dry and then staining the preparation with Giemsa stain. Vaginal smears were obtained by flushing a drop or two of water into the vagina with a pipette. Care had to be taken not to irritate the vaginal wall with the pipette, since such irritation occasionally induced pseudopregnancy. Vaginal smears were dried and stained with Giemsa stain.

Pseudopregnancy was electrically induced by two small platinum electrodes mounted in a plastic cylinder which could be inserted a quarter of an inch into the vagina. Electrical stimulus was supplied by two 1½-volt dry-cell batteries connected in series to an inductorium.

The rats, which were usually very sensitive to handling, showed little apparent ill effect when handled in the following manner. A rectangular box made of hardware cloth and open at one end was placed over the caged rat, and a temporary door then covered the open end. The animal, thus captured, was under little restraint, since the box was large enough to allow it to turn around. A large bag made of fish netting was placed over the temporary door. When the door was removed, the rat, with slight encouragement, usually walked from the box into the net bag, where weight, measurements, vaginal smears, and other records could be taken while the animal was only momentarily under restraint. Between brief

handlings the rat was free to move about in the bag. An additional advantage of this method was that the person handling the animal could more easily avoid being bitten and therefore did not need to be encumbered by gloves.

GROSS ANATOMY

MALE REPRODUCTIVE SYSTEM

The anatomy of the adult male genital system of *Rattus assimilis assimilis* is essentially like that of *R. norvegicus* as outlined by Greene (1935), and so will not be discussed in detail. In sexually active adults the testes average 27 mm. in length. Variations of 3–4 mm. above and below this average correspond in general with the variation in total body size. The weight range is 2.0–3.5 grams per testis, averaging 2.4 grams, and the testes of a pair usually vary not more than 0.2 of a gram from each other. The testes of the adult, upon dissection, are usually posterior to the inguinal canal; however, the maximum degree of descent into the scrotum, as observed in the living animal, was frequently associated with sexual aggression toward the female.

Average weight of an epididymis is 0.55 of a gram, with a range of 0.40–0.76 of a gram. Each of a pair of epididymides usually weighs about the same. Cranial and caudal portions of a single epididymis are also approximately the same size and weight. Average weight of the seminal vesicles is about 1 gram, although in males of breeding condition the weight can vary from 0.63 of a gram to 2.37 grams.

The perineal region is sparsely covered with short unpigmented hair about 8 mm. in length. Black pigment covers the posterior part of the scrotal area and the pigment may or may not envelop the anal opening. In the specimens examined, this pigmented portion is consistently restricted in extent; the area averages 10 mm. anteroposteriorly and 14 mm. from side to side.

Average distance between penis and anus is 29 mm. The uneverted penis is 8 mm. long, whereas in *Rattus norvegicus* it is 5–6 mm. long. When everted on a freshly dead specimen, the penis of *R. a. assimilis* is 15 mm. long from prepuce to tip and 23 mm. long from base to tip. In *R. norvegicus* it is 9–10 mm. long from prepuce to tip and 23 mm. long from base to tip.

Except for its additional length, the fleshy portion of the penis is very similar in its configuration to that of *Rattus norvegicus* as described and sketched by Argyropulo (1929:148–152). The distal portion of the penis contains a baculum composed of two distinct osseous portions (fig. 8). The basal ossification is either translucent or chalk white; there is no apparent correlation between this quality of the bone and the age of the animal in the adult category. Younger specimens were not examined. The distal ossification is chalk white in all the adults examined.

Average length of the baculum of *Rattus assimilis assimilis*, as determined from 18 specimens, is 7.5 mm. (range 7.0–7.9 mm.). Measured from the dorsal face the proximal ossification averages 4.2 mm. in length (range 3.7–4.5 mm.) and from its ventral face, 4.7 mm. (range 4.2–5.0 mm.). The distal ossification averages 3.1 mm. in length on the dorsal face (range 3.0–3.3 mm.) and 2.6 mm. on the ventral face (range 2.3–2.8 mm.). The basal ossification abuts its oblique end on that of the distal ossification, forming a slight angle between the two portions such that the entire baculum is slightly concave on its dorsal surface. The con-

nection between basal and distal ossifications is easily separated in the course of their preparation.

Chaine (1926) states that the total length of the baculum of *Mus rattus* (now *Rattus rattus*) is 3 mm. and that that of *Mus norvegicus* (*Rattus norvegicus*) is 5 mm. His figures, however, give no structural detail and even suggest that the distal ossification may not have been included in his measurements. Argyropulo (1929) gives no written dimension, but if the millimeter rule on page 150 is actually scaled to the figure of the baculum of *R. norvegicus* on page 149, as is indi-

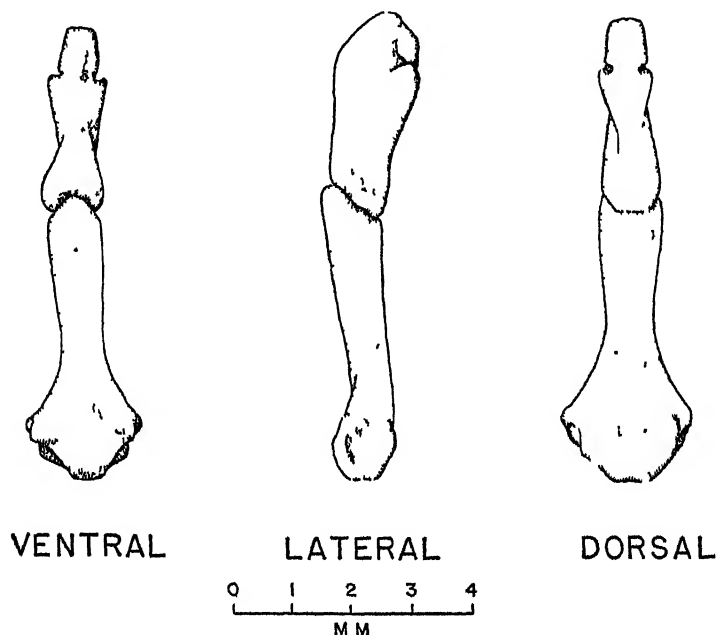


Fig. 8. Baculum of adult *Rattus assimilis*.

cated, the total length of the baculum is about 3.5 mm. From this figure it appears also that the baculum of *R. norvegicus* has two osseous portions. The present author prepared several bacula from the Long-Evans laboratory strain of *R. norvegicus* and found that the baculum averaged 8.5 mm. in total length. Despite the apparent range of variation in the total length of the baculum of this species, a character which may not in itself distinguish it from *R. a. assimilis*, the bone appears to be considerably heavier at the basal end than is that of *R. a. assimilis*, and it differs substantially in the shape of the distal portion.

Under laboratory conditions there is no correlation between the length of the baculum and age in *Rattus assimilis assimilis* 5 or more months old. Measurements for this species were obtained from specimens 5–21 months old, averaging 10 months old. A detailed account of the baculum of this species is given here, not only because it is an important sexual character but also because its conformation may prove to be an important taxonomic aid in the further evaluation of the complex group of species of *Rattus* endemic to Australia. Burt (1936) sug-

gests that the baculum is, of the skeletal parts, one of the least likely to be subject to external stresses and strains and may therefore be most likely to reveal the true affinities of mammals, particularly at the species level. In anticipation of this it is hoped that future work with the Australian rodents will include the preservation and detailed description of the bacula.

FEMALE REPRODUCTIVE SYSTEM

The internal anatomy of the adult female genital system of *Rattus assimilis assimilis* closely resembles that of *R. norvegicus* (Greene, 1935). Each uterine horn in the nonpregnant individual averages 24 mm. in length, the average vaginal length is 17 mm., and the average ovary length, taken as an anteroposterior measurement, is about 4 mm. As in *R. norvegicus*, the periovarial membrane surrounds the ovary, thus making it highly unlikely for ova to disperse anywhere but into the oviduct.

The external genitalia, however, in both male and female *Rattus assimilis assimilis* differ markedly in some dimensions from those of *R. norvegicus*. Unlike that of *R. norvegicus*, the clitoris of *R. a. assimilis* is a conspicuous structure. The posterior aspect of the base of the clitoris lies about 3 mm. anterior to the vaginal orifice, and the structure is 7–9 mm. long. In *R. norvegicus*, however, it is normally no longer than 4 mm. The clitori of eight specimens of *R. a. assimilis* were cleared in potassium hydroxide and subjected to an alizarin red bone stain. There was no evidence of an *os clitoridis* in any of the preparations, nor has this bone been found in *R. norvegicus* (Simokawa, 1938).

A sparse covering of unpigmented short hair covers the perineal region. The perineal skin may or may not contain black pigment, although in the females examined this pigment was usually present. The pigment varies from individual to individual in extent, but it usually envelops the vaginal orifice, including the lips, and extends posteriorly to the anus, but rarely surrounds the anal opening.

There is much disparity in the literature concerning the mammary formula of *Rattus assimilis*. Tate (1936:523) under his *R. assimilis* group gives the formula as 0–2, which is interpreted as no pectoral teats and two inguinal teats on each side, a total of four. According to Tate (1951) he meant to give the formula as 1–2=6 in his 1936 publication. Tate (1951:201) then further corrects this figure and states that 2–3=10 is the mammary formula of *R. a. assimilis* and tentatively assigns 1–3=8 as the formula of *R. a. coracius*. The formula 2–3=10 is denoted by Tate (1951:201) as a group character for his *R. assimilis* group despite the fact that only one of the three subspecies of *R. assimilis* which he recognizes definitely agrees with this group generalization. *R. a. coracius* appears not to have this formula, and the teat count and arrangement are unknown for *R. a. manicatus*. It therefore seems misleading to make a generalization for this group.

The importance of determining the mammary formula from fresh material rather than from dried skins cannot be overemphasized. In nonlactating individuals particularly, the teats are inconspicuous even on living individuals, and in all adult specimens they are well concealed beneath the dense long ventral fur.

In the present study the mammary formula of 39 specimens of *Rattus assimilis assimilis* was determined from the living or freshly dead animals, and invariably

the count was $2 - 3 = 10$. The specimens used all stem from one locality; so this does not preclude the possibility that the mammary formula of this subspecies may vary geographically. Variations from this count are recorded on a few museum skins examined (American Museum of Natural History, 65855, 65863, and 65875), but as the counts may have been made on dry skins, they are not seriously considered here, especially since the total number of teats in each of these counts is less than 10.

That the mammary formula does vary within a species of *Rattus* is reported for *R. rattus* (Delano, 1924); and Ellerman (1949:189-190) lists several variations of mammary count within species of this genus. Variation in *R. rattus* at even the sibling level was obtained in the present field study. Of the two females from a field-bred, laboratory-raised litter, one had the formula $2 - 3 - 10$ and the other $3 - 3 = 12$. There is no uncertainty here in the count, since the teats were very conspicuous in young rats before the ventral body hair grew out. Tate (1951) feels, however, that the mammary formula of the endemic East Asian and Australian *Rattus* is more stable than Ellerman suggests.

Not only is the number of teats constant in the *Rattus assimilis assimilis* examined in this study, but also their arrangement in the mammary line. Of 17 females measured immediately after death whose body length (exclusive of tail) ranged from 154 mm. to 198 mm., the teat arrangement was as follows. From the vagina to the posterior inguinal teat the straight-line measurement varied from 12 mm. to 18 mm., with the mode at 15 mm. From this teat to the middle inguinal teat the straight-line measurement varied from 6 mm. to 13 mm., with the mode at 9 mm. From the middle inguinal teat to the anterior inguinal teat the straight-line measurement ranged from 11 mm. to 22 mm., with the mode at 18 mm. The distance between the anterior inguinal teat and the posterior pectoral teat varied from 31 mm. to 49 mm., with the mode at 41 mm.; and the distance between the posterior and anterior pectoral teats ranged from 18 mm. to 33 mm., with the mode at 23 mm.

In a single individual, measurements of the right and left mammary lines were almost identical. The difficulty of obtaining precise measurements of external body parts attached to the loose skin of the venter may in part account for the variations in measurement. It is felt, nevertheless, that the maximum error in these measurements does not exceed 5 mm. The only measurement directly correlated with body length was the distance between anterior inguinal teats and posterior pectoral teats.

The teats can be divided into two discrete units in a mammary line, the inguinal set and the pectoral set, within each of which there is no direct spatial correlation with the total body length. Internally, however, mammary tissue may extend as a continuum from the abdominal to the pectoral region. This is particularly evident in animals which are lactating or have recently been lactating.

BREEDING BEHAVIOR

As is customary in the laboratory breeding of many mammals, when members of *Rattus assimilis assimilis* were paired, the female was introduced into the cage of the male. The females usually exhibit stronger territoriality than do the males,

and when paired in this manner less conflict is likely to arise. When space permitted, both animals were introduced to a new cage, which seemed to further minimize fighting.

Most of the pairing was done in daylight hours and no sexual activity was observed at this time, even among pairs which bred frequently and had been caged together many times before. Copulatory activity was seen only at night. The lights which were turned on for observation did not appear to inhibit their activities seriously. Attempts at copulation, with the male mounted on the female, were seen frequently during the first two years of the study, only rarely during the third year, and never during the fourth year.

The male mounts the female with his forearms clasped about her lower abdomen and his chin resting on her mid-dorsum, and when losing his grip or balance he repeats the mount immediately. The female may or may not exhibit lordosis during these attempts. When in lordosis she permits her hind legs and entire hind quarters to be picked up by the male while the male licks her genitalia. These attempts are frequently accompanied by the almost continual squealing of the female. Such copulatory activity may continue for at least 30 minutes.

During the many observations made, however, not once was a successful coitus witnessed. Vaginal smears taken of these females the following morning only occasionally contained sperm. Also, a single pair may attempt copulation four or five nights in a row, with the female seemingly receptive on each of these nights. It appears then that copulatory activity, although not ejaculation, is practiced under captive conditions much more commonly than the frequency of sperm retrieval from the vagina would suggest, and that both members of the pair are stimulated into this activity regardless of whether the female is in estrus. Successful coitus, however, as determined by sperm retrieval from the vagina, occurs only when the female is in estrus. No exception to this was found in the present study.

The interscapular area and the adjoining nape of the neck appear to be associated with behavior during sex activities. Both before and after attempts at copulation one rat will frequently lick or pull the hair of this region from the other rat: Such activity occurs repeatedly in newly mated pairs; one member will actually chew off the hairs in this region while the other remains crouched and often squeaking. The crouching rat rarely attempts to defend itself even when, as often happens, the skin is torn off. The occurrence of badly damaged neck and scapular regions was surprisingly high (approximately 20 per cent of the matings) and, unless the pair were separated, the damage would usually be continued until the submissive partner was killed.

This behavior occurred mostly at night and for brief periods; ordinarily there were four or five nights of such activity before the skin itself was attacked. Either sex may be the attacking member, but once the animals are paired, even after separation and re-pairing, the same member usually exhibits dominance. No evidence of hair cropping or skin injury of this nature was ever witnessed in the field, however; so both this and perhaps also the extra-copulatory attempts may stem from close confinement.

The number of injuries in the neck region dropped significantly with the de-

crease in copulatory activity observed during the third year of captivity; and, in the fourth year, when no sex activity was observed, there was also no occurrence of neck damage. Such correlation further substantiates the suggestion that under captive conditions this damage is a result of behavior connected with sex activity.

BEHAVIOR DURING PARTURITION AND LACTATION

Parturition was observed only once. A female giving birth to her first litter sat with her hind legs tucked under her, forelegs in front to support her body, and tail to the side. The first young one had emerged by 3:00 P.M., when the observations began. The second was seen emerging rump first at 3:06 P.M. As it was brought forth, the female turned from side to side and also turned her head down over the venter and licked the young rat as it was being born. Just before it had completely emerged, the female stretched her body and underwent several deep abdominal contractions. By 3:08 P.M. the newborn rat was free from the parent except for its connection to the unshed placenta via the umbilical cord. The female licked the young rat intensively but did not pick it up. More abdominal contractions quickly followed and by 3:09 P.M. the placenta was shed. The female immediately turned to the placenta and ate it and then ate the attached umbilical cord up to its connection with the young rat. At 3:16 P.M., after the female had vigorously licked her genital area, another young one was born rump first and emerged completely within ten seconds. The placenta was shed immediately after birth. Again the female ate the placenta and the cord up to the attached young one and then washed it.

Breathing movements were observed in the young immediately after birth. None appeared to be enclosed in an amnion at birth. It is highly probable that intensive licking of the young during birth by the female broke this membrane before parturition was complete. The female made no vocal sounds during or after parturition. After the three young had emerged, the female assembled them in a nest and crouched over them.

Lactating females spent a large part of the day crouched over their young. Whenever a young rat less than three weeks old wandered from the nest, or lost its hold on a teat when the female was wandering about the cage, the female would take it in her mouth and place it back in the nest. Young less than a week old were frequently carried by the head alone, which often bore small cuts and scars from this method of conveyance. When a female left the nest for any length of time she would arrange nesting material over the young and thus conceal them from view. This rearranging of nesting material continued until the young were three weeks old.

THE MALE CYCLE

Harrison (1955: 453-454) has found that some of the adult males of the Malayan *Rattus mülleri*, *R. sabanus*, *R. rajah*, and *R. whiteheadi* exhibit a seasonal cycle in sperm production. From October to March the testes of these individuals become reduced in weight and there is a decided increase in nonfertility; from April to September testicular weight increases and the proportion of nonfertile individuals decreases. These data are from field-caught specimens. McDougall (1946a), however, finds that in the Queensland *R. conatus* the male is capable of breeding

throughout the year, and that breeding activity seems to depend on the condition of the female. The ascent of the testes of *R. conatus* in June and July under both laboratory and field conditions has no apparent effect on the fertility of the rodents at that time. Perry (1945) finds no evidence of seasonal variation in sperm production in the wild brown rat, *R. norvegicus*.

In the present investigation the approximate size of the testes, as judged externally by examination of the scrotal region, was used as a gross morphological indicator of fertility for the living *Rattus assimilis assimilis*. This was supplemented for verification of the presence of sperm by occasional biopsies of epididymal portions. A few specimens were sacrificed at various times of the year. Sections were made of the testes from all individuals upon death.

The testes were approximately an inch long in all but two of more than 50 adults examined, and these two rats were not fertile. Sperm were invariably retrieved from the epididymis of rats with sizable testes, and histological preparation of the testes showed evidence of active sperm production. There is no indication by these criteria that the adult male *R. a. assimilis* experiences a cyclical production of sperm in the laboratory.

The testes appear to move from inguinal to scrotal position and back again from day to day. Regardless of the position of the testes, the introduction of a female into the cage usually elicits maximum testicular descent from the male at any time of the year. It is concluded that the male *R. a. assimilis* are, at least under laboratory conditions, continuously fertile throughout adult life.

THE FEMALE CYCLE

THE ESTROUS CYCLE

The vaginal cycle.—The sexually mature female *Rattus assimilis assimilis* experiences an estrous cycle averaging 4.5 days in duration. This cycle was determined from 1603 vaginal smears of 37 individuals. All but four cycles lasted 4–5 days. Of these four, three were 6-day cycles, of which one was the interval between postpartum estrus and the following estrus in a nonlactating individual. The fourth was a 3-day cycle between postpartum estrus and the next estrus in another nonlactating individual. There was no correlation between age and the fluctuation between the 4- and the 5-day cycle in actively reproducing females. The cycle of an individual varied between 4 and 5 days over a period of two or three weeks. McDougall (1946a) stated that the Queensland *R. conatus* has a 4-day estrous cycle with a maximum variation of 3–6 days. Long and Evans (1922) found that the laboratory rat *R. norvegicus* has a cycle of 4.8 days.

Proestrus, characterized by the presence of nucleated epithelial cells of uniform size in the vaginal smear, lasts 10–14 hours. The lips of the vaginal orifice tend to be slightly swollen, the swelling being more pronounced toward the end of this stage.

Estrus, typified by cornified epithelial cells, lasts about 24 hours. The vaginal lips are swollen, and mating appears to occur at the early part of this stage only. Mating may even occur before many of the epithelial cells have become truly cornified. In *Rattus norvegicus* heat is more closely associated with the beginning of cornification than with the end of it (Young *et al.*, 1941). The latter part of

this stage in *R. a. assimilis* is probably comparable to the Long and Evans Stage III, or Postestrous Stage, for the loose cornified epithelial cells and pavement nucleated cells are very abundant and mating does not usually occur.

Metestrus, the stage at which cornified cells and leucocytes are retrieved from the vagina, lasts not longer than 10 hours and usually less. The lips of the vagina have lost their swollen appearance at this stage.

Diestrus, characterized by the presence of leucocytes and nucleated epithelial cells, usually lasts 50–60 hours. The vaginal lips are not swollen at this time.

The foregoing data were obtained from four rats in prime adult condition. The data indicate that in both total length of cycle and in stages within the cycle, *Rattus assimilis assimilis* has an estrous cycle very similar to that of *R. norvegicus*.

Long and Evans (1922) maintain that the occurrence of a regular estrous cycle in *Rattus norvegicus* is a manifestation of the animal's physiological well-being. If this be true also for *R. a. assimilis*, it may explain the increasing display of grossly irregular cycles during the third and fourth years of the colony's existence. Even animals less than a year old tended to exhibit long periods of cornified cells only, or five to ten days of cornification terminated by a day or two of leucocytes and epithelial cells and then another interval of complete cornification. Vitamin A deficiency will induce permanent cornification of the vaginal mucous membrane in *R. norvegicus* (Evans, 1928). No tests were made for this deficiency in *R. a. assimilis*. The diet on which the animals were maintained, Diet 1 (Nelson *et al.*, 1955), however, contains 1 per cent fish oil, a Vitamin A D concentrate. Whatever the cause, smears of noncyclical nature were retrieved during the latter part of the colony's existence, and breeding activity ceased by the time the colony was in the latter part of its third year.

The uterine cycle.—The histological changes of the uterus of *Rattus assimilis assimilis* associated with the estrous cycle appear to be very similar to those described for *R. norvegicus* (Long and Evans, 1922) and so will not be discussed further. Maximal uterine distention occurs at estrus; the lumen is then filled with fluid. After estrus the diameter of the uterus is reduced 50 per cent or more and then builds up to the next estrus. This is in accord with observations made on *R. norvegicus*.

The ovarian cycle.—The average number of corpora lutea associated with a single estrus is 7, but there may be as many as 11 or as few as 3. A single ovary may yield from 1 to 7 per cycle (pl. 3, b). A fully formed corpus luteum measures 1 mm. or more in diameter and a fully formed follicle measures 0.8–0.9 mm. These data were obtained from gross examination of fresh ovaries and from serial sections of paired ovaries of 19 rats which were exhibiting regular vaginal cycles.

Although it is possible that more than one generation of corpora lutea was represented in some counts, the author feels reasonably sure that this did not occur. The corpora lutea change in texture as they age (Hall and Davis, 1950), and the only time when two sets of corpora lutea are likely to be comparable in size is on the day following an ovulation.

Perry (1945) states that for the wild *Rattus norvegicus* the number of corpora lutea in the ovaries corresponds exactly with the number of ova released. This appears to be true for *R. a. assimilis* also, since in two counts of newly implanted

embryos the number of embryos in each uterine horn was identical with the number of the most recently formed corpora lutea of the corresponding ovary.

POSTPARTUM ESTRUS

One estrus, the postpartum estrus, usually occurs between parturition and the onset of lactation anestrus. Vaginal smears were taken on Day 0, the day of parturition, after 16 parturitions, and once every succeeding 24 hours. The data were obtained from 12 individuals and the smears continued for six days after each parturition. Postpartum heat was recorded for 13 of these 16 occasions. On the three times in which estrus was not found it is possible that the animals went through heat during one of the intervals between smears. Since the average length of postpartum heat in *Rattus norvegicus* is 10 hours (Asdell, 1946), this supposition seems reasonable. The average duration of postpartum heat in *R. a. assimilis* was not determined, but it appears to be less than 24 hours, for cornified smears were never obtained on successive days at this time.

The time of onset of postpartum heat varies appreciably in *Rattus assimilis assimilis*. Postpartum heat was never recorded on the day of parturition. It occurred six times on Day 1, five times on Day 2, and twice on Day 3. The mean interval was 1.7 days, or about 41 hours after parturition. This differs markedly from *R. norvegicus*, in which the average interval was 18.5 hours, ranging from 4 hours to 36 hours. That ovulation accompanies this postpartum heat was confirmed seven times in the Smith College colony when the female was successfully impregnated during this heat and subsequently bore a litter. In females whose litters die between parturition and Day 5, the interval between postpartum estrus and the following estrus may fall short of or exceed by one day the regular estrous cycle of 4-5 days.

ANESTRUS

Lactation anestrus.—The very high loss of litters in the present study discouraged more than minimal disturbance to the lactating females; therefore, only four records were obtained during lactation. Each of four individuals exhibited a period of lactation anestrus after the postpartum heat. Lactation anestrus, typified by leucocytes and a few epithelial cells in the vaginal smear, is here defined as the period from postpartum estrus to the onset of the following estrus. The shortest interval of lactation anestrus was 20 days and the longest was 24 days. All litters were of three or four young; so the effect, if any, of litter size on the duration of lactation anestrus, as reported for *Rattus norvegicus*, was not detectable. In fact, there was a litter of four in the 20-day interval, and a litter of three in the 24-day interval. This 20- to 24-day interval is shorter than the lactation anestrus of *R. norvegicus*, which may last 25-40 days after parturition (Long and Evans, 1922). The disparity in the length of lactation anestrus in the two species may be correlated with the normal litter size of each species; *R. norvegicus* usually raises at least twice as many young as *R. a. assimilis*.

Lactation anestrus is of common occurrence in members of the family Muridae (Asdell, 1946), to which these rats belong, but the other Australian murid for which reproductive data are known, *Rattus conatus*, does not experience lactation

anestrus (McDougall, 1946a). McDougall states that there is no interruption of ovulation or estrus during lactation in the wild *R. conatus*.

Nonlactation anestrus.—During the first two years of the colony's existence, when the females were at the height of breeding activity and going through normal estrous cycles, multiparous individuals would occasionally enter periods of anestrus lasting 10–44 days. These periods frequently followed soon after the weaning of a litter. Brambell and Davis (1941) found such anestrus periods in *Rattus (Mastomys) coucha*, particularly after an interval of active breeding, and considered them to be resting periods. Whereas in *R. coucha* these periods are associated with seasonal breeding inactivity, in *R. a. assimilis* there is no correlation between season and the onset of anestrus in the laboratory. No data of this nature are available for these rats in the field, however.

These periods of anestrus must be interpreted with caution: no proof is available that they are normal, even in the laboratory colony. It is possible that the very mechanics of taking a vaginal smear may stimulate the rat into pseudopregnancy. Yet the fact that these anestrus periods exhibit a wide range in duration supports the view that they are normal. In the electrically stimulated pseudopregnant rats, in contrast, the duration of anestrus appears to be narrowly restricted.

PSEUDOPREGNANCY

Pseudopregnancy was induced in five females after electrical stimulation of the vaginal wall and cervix when they were in estrus. The pseudopregnant cycle lasted 15–17 days: in two rats for 15 days, in two for 16 days, and in one for 17 days. According to Shelesnyak *et al.* (1940) the length of pseudopregnancy in *Rattus norvegicus* when the vagina is electrically stimulated is 11.03 days; Long and Evans (1922) report the modal length of the cycle to be 12–14 days. From the small sample used it would appear that *R. a. assimilis* has a longer pseudopregnant cycle than does *R. norvegicus*. Pseudopregnancy could not, however, be induced in *R. conatus* by artificial stimulation (McDougall, 1946a).

In the four cases of infertile copulation recorded from *Rattus assimilis assimilis*, where sperm were retrieved from the vagina but no pregnancy ensued, it was surprising to find that pseudopregnancy was not induced. Since these infertile copulations were recorded only in the third and fourth years of the colony's existence, it is possible that the females were not physiologically normal. Two of these copulations were preceded by anestrus and two by regular cycles according to readings from the vaginal smears.

STERILE CYCLE

Following the time of vaginal perforation in young *Rattus assimilis assimilis*, the animal may or may not exhibit a normal sequence of vaginal cycles. In three of eight animals examined, the normal vaginal cycle was initiated immediately after the perforation of the vagina. In the other five the normal cycle did not occur until 14–22 days after vaginal perforation. In all eight animals some irregularity, in the form of several successive days of cornified smears or several days of epithelial cells and leucocytes in the vaginal smear, was exhibited at

some time between vaginal perforation and the subsequent four-week period. Although males were made available upon female puberty, no occurrence of pregnancy was ever noted at this time. The irregular cycles and lack of pregnancy during this interval suggest that after vaginal perforation a period of sterility occurs which may last a month or less.

McDougall (1946a) found that in *Rattus conatus* ovulation occurs $3\frac{1}{2}$ – $4\frac{1}{2}$ weeks after vaginal perforation. Long and Evans (1922) report that the first fertile copulation occurs, on the average, 16 days after vaginal perforation in *R. norvegicus*, and that ovulation may or may not coincide with the opening of the vagina. Greenwald (1956) describes the sterile cycle associated with puberty in *Microtus californicus* as a "tuning-up" stage before a balance has been established in the pituitary-gonad relationship. This is probably the explanation for the sterile cycle in *R. a. assimilis* as well.

GESTATION

The gestation period is here defined as the interval between the time of retrieval of sperm in the vagina and the time of parturition. In *Rattus assimilis assimilis* the gestation period lasted 22–24 days as recorded a total of 20 times in 15 rats. The average gestation period is 22.8 days and the mode, incorporating 60 per cent of the individuals, is 23 days. Long and Evans (1922) report that 90 per cent of the *R. norvegicus* tested have a gestation period of $21\frac{1}{2}$ –22 days, with an over-all average of 21.8 days. The gestation period in *R. conatus* lasts 20–27 days, with the modes occurring at 21 days and 22 days.

The longer gestation period of the lactating female *Rattus assimilis assimilis* suggests that delayed implantation of the embryos, which causes prolonged gestation in *R. norvegicus* (Krehbiel, 1941), is encountered in *R. a. assimilis* also. When the female is nursing a litter from birth to weaning, the interval between births ranges from 28 days to 32 days. The size of the nursing litter may influence the length of delay before implantation, since the largest nursing litter (six) was associated with the 32-day period. A litter of four, however, coincided with a 28-day period, and a litter of three with a 30-day period; so perhaps the influence of litter size is negligible below a certain number. A 25-day gestation period was recorded with a nursing litter of five, which declined to two 6 days after birth, to one 7 days after birth, and to none 11 days after birth. A 23-day gestation period was associated with a litter of four, which declined to three 9 days after birth and to none 10 days after birth. On two other occasions when litters of five and seven young were born and then died or were removed 6 days and 4 days, respectively, after birth, the pregnant female gave birth to the next litter within the normal period of gestation. It appears, then, that the gestation period of a lactating female's litter is not affected by the existence or size of the nursing litter until after the first week of pregnancy. These data are taken from the Smith College colony where, unlike the situation at the University of California colony, the male remained with the female during her postpartum heat.

Three nonlactating females were sacrificed in order to determine the time of implantation during the regular gestation period. No implantation of embryos had occurred in the female sacrificed on the fifth day of pregnancy, but both

females sacrificed on the sixth day of pregnancy had embryos implanted in the uterine wall. The sixth day is also the time at which implantation occurs in *Rattus norvegicus*. The time is not known for *R. conatus*.

PARTURITION

The time of parturition, within six hours, is known for 65 per cent of the litters born in captivity. Parturition tends to be associated with a particular period in the daily cycle of *Rattus assimilis assimilis*, for 80 per cent of the time-recorded births occurred between 2 P.M. and 8 P.M. Asdell (1946) reports that parturition usually occurs in the afternoon in *R. norvegicus* and least often between midnight and 6 A.M.

The sexes were recorded of all young surviving the first 24 hours. There were 51 males and 52 females, a ratio determined from survivors of 56 litters; 41 other litters are known to have been produced, but they were destroyed immediately after birth or soon thereafter, and no sex determinations of these could be made. The 50:50 ratio of young produced in the laboratory agrees with the ratio obtained from the population of adults in the field, and there is nothing to suggest that under natural conditions the ratio would deviate markedly from this point.

The number of young per litter, as determined from the examination of litters on Day 0, ranged from 1 to 7 for 79 litters, with an average of 3.81 per litter. The mode, incorporating 24 per cent of the litters, was 4. From the remains of young found in the cages, 18 other litters are known to have been produced. In the Smith College colony 24 litters were recorded, averaging 4.21 young per litter. The lower limits of the range may well be influenced by the destruction of one or more young soon after birth.

Examination of a few pregnant females suggests that the prenatal number of embryos is slightly higher: a maximum of 9 newly implanted embryos was recorded in one instance; 6 newly implanted embryos were also recorded, and a field-caught animal was carrying 6 embryos judged to be about two weeks old. The average number of ova shed per estrus is 7 according to the corpora lutea count, and ranges from 3 to 11. In *Rattus norvegicus* loss of ova and fetal atrophy reduce the potential litter size by about one-third (Long and Evans, 1922), and by at least 25 per cent for shore-dwelling wild *R. rattus* (Watson, 1950). The number of ova shed and the number of early embryos compared with the number of young produced at birth suggest that loss of ova and/or fetal resorption account for a prenatal loss of about 40 per cent in *R. a. assimilis*.

Within the genus *Rattus*, *R. a. assimilis* falls in the lower end of the spectrum in average number of young per litter as well as in maximum number known to be produced. In this respect it resembles *R. exulans*, a widespread Indo-Pacific rodent, and also many of the Malayan species of *Rattus* (Harrison, 1955). The common Queensland cane rat, initially identified as *R. culmorum* and later as *R. conatus* (Troughton, 1939), has an average litter size of 7.5 (Gard, 1935:598) for the first pregnancies and under captive conditions an over-all average of 5.2 (Sawers, 1938:1093); in the field it averages 6.0 (McDougall, 1946a:35). A litter of 14 has also been recorded for this species (Sawers, 1938:1093).

The small range in litter size of *R. a. assimilis* is doubtless one reason for setting it apart from *R. conatus* as an animal that experiences very limited fluctuations of population size within a short interval of time. *R. assimilis* has to date never been reported to occur in the sporadic plague numbers comparable to those of *R. conatus* (McDougall, 1944b).

LACTATION AND WEANING

The female *Rattus assimilis assimilis* begins to nurse her young soon after parturition, and usually within eight hours after birth the young have milk-filled stomachs. All teats are ordinarily in use except when the litter size is reduced to less than three. Then the pectoral set, or part of it, is abandoned. When the litter is reduced to one during the first 1½ weeks the stimulus to maintain lactation drops below the threshold; the female, with rare exception, ceases to produce milk and the young rat dies.

The female normally lactates for the first 3 weeks after parturition, and lactation does not taper off until the litter is in its fourth week. If the young are removed at 21 days, they may lose as much as one-quarter of their body weight during the next few days. The young have just begun to sample solid food at this time and their physiological adjustment to a completely solid diet is sub-optimal at 21 days. The death of a litter of four when 4½ weeks old was probably due to their inability to adjust to a solid diet, for none had gained weight after removal from the parent at 21 days. However, when the young are removed at 3½ weeks or at 4 weeks after birth, they decline in weight, if at all, only a gram or two and then continue to gain weight; when the young are kept with the female indefinitely they are not seen to nurse after the fourth week. Thus, at least under laboratory conditions, weaning occurs in the latter part of the fourth week after birth.

COLONY SIZE AND REPRODUCTIVE SUCCESS

Comparison of the two colonies.—The University of California colony and the Smith College colony of *Rattus assimilis assimilis*, although fed and housed under different conditions (Horner and Taylor, 1958), show striking similarities in their pattern of growth and decline. Both colonies began to breed within three months of their arrival in the United States, and both increased in size to a certain point and then declined immediately; the peak in size occurred at about the mid-point in time of the colonies' existence. Litters were produced for two years in the Smith College colony and for three years in the University of California colony. After that, absolutely no breeding activity was observed in either colony. In both colonies there was a sharp drop in rate of litter production before maximal size was attained (fig. 9). Only 17 per cent of the third generation of females produced young, whereas 67 per cent of the parental (wild-caught) females, 75 per cent of the first generation, and 61 per cent of the second generation produced litters. Not only did the litter production of the third generation of females decline markedly, but the combined litter production of parental, first, second, and third generations dropped off as the colonies grew older. This suggests that whatever cumulative deficiency, dietary or otherwise, might have caused the

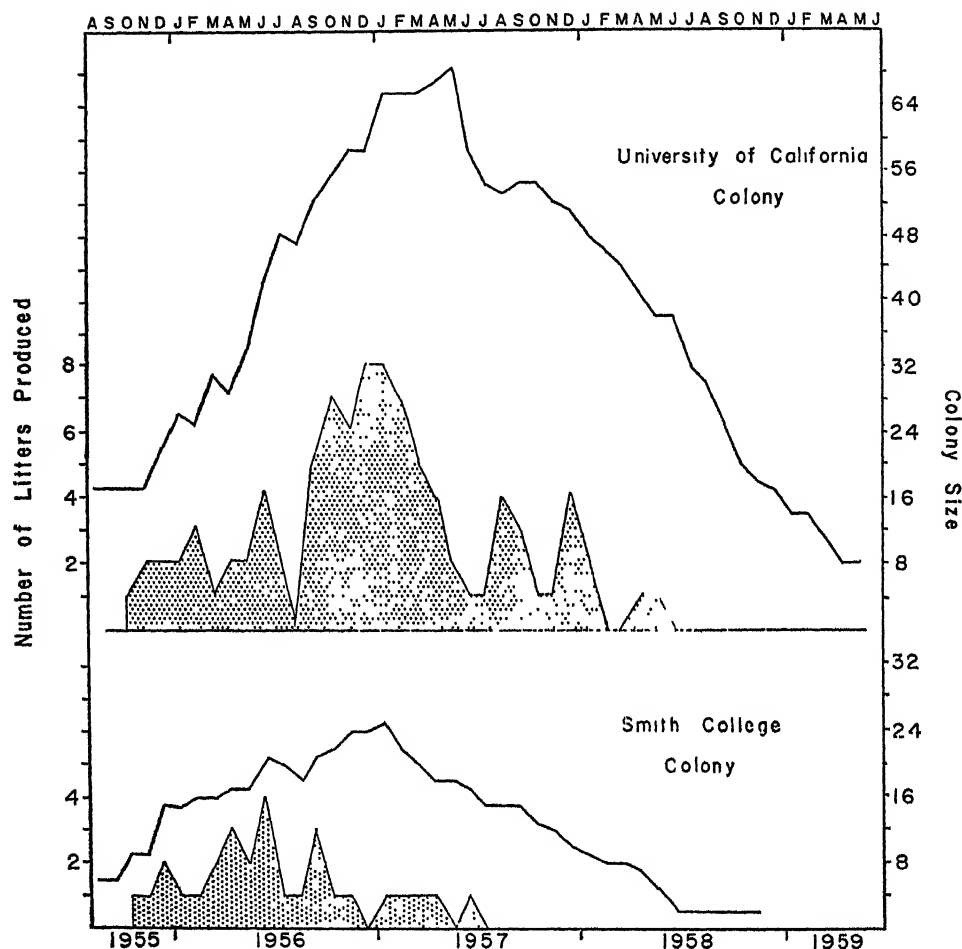


Fig. 9. Relation of litter production to colony size. Stippled area represents number of litters per month; clear area, number of rats in the colony per month.

reproductive decline, the deficiency was a function of time and was exhibited in a single individual as well as in successive generations.

Seasonal variation.—Breeding occurs throughout the year under laboratory conditions. Evidence has already been presented that breeding occurs during every month of the year in the field, with the possible exception of July. If under laboratory conditions there was a differential output of young which could be correlated with the season of the year, it was masked by the rapid growth and decline of each colony. Reproductive effort may increase at the time of maximum rainfall in the field, but this seasonal increase is probably a response to rainfall or to some other environmental factor, since it was not duplicated in the laboratory.

Breeding age.—The vagina opens between 35 days and 57 days and at an average of 46 days. Body weight at this interval varies from 37 grams to 73 grams and

averages 56 grams. Perforation of the vagina is not a sign that sexual maturity has been attained. Females less than 50 days old, regardless of the condition of their vaginæ, have not begun to ovulate and have not exhibited regular vaginal cycles. The periphery of the immature ovary contains many small follicles measuring up to 400 microns in diameter (pl. 3, a). Ovulation usually begins early in the third month and is accompanied by a stabilization of the vaginal smear pattern to a series of regular cycles. Only one female was successfully impregnated before the third month and she bore a litter when 68 days old. Another female bore her first litter at 86 days of age and another at 93, but these were exceptional cases. The average age at which a female produced her first litter was 4½ months, as determined from 27 females raised in captivity.

The average age at which a female ceased to produce young was 12 months. The oldest female to bear a litter was a field-caught animal which gave birth 24 months after she had been removed from the field as a young adult. Three females bore litters at 16 months of age. There seems to be no direct correlation between the age at which breeding ceases and the number of litters produced.

The average life span of females in captivity is 16 months; the longest life span recorded for a laboratory-bred female is 35 months, and for a field-caught female 37 months in captivity plus at least 4 months in the field. The physiological life span in captivity therefore exceeds the age at which young are normally produced. The female of *Rattus assimilis assimilis*, like that of *R. conatus* and *R. norvegicus*, experiences reproductive regression and senility in the laboratory.

The young male of *Rattus assimilis assimilis* becomes sexually mature when about 2½ months old. The youngest to sire a litter was 70 days old. Another male sired a litter when 79 days old and a third when 82 days old. Although females were present with the males from weaning on, the males did not usually breed until they were 4 months old. For the first 6 weeks after birth the testes are very small and increase in size slowly. At 4 weeks a testis weighs 0.1–0.2 of a gram (pl. 4, a) and at 6 weeks 0.3 of a gram. Growth is then rapid until at 2 months the testes are prominent in the scrotal area. Sperm are not produced up to this time, and the individual tubules of the testis are small in diameter. At 6 weeks the tubule walls thicken and meiotic figures become prominent. Sperm are present in the tubules 3–4 weeks later, and the animal is sexually mature (pl. 4, b). At 6 weeks the average body weight is 54 grams; at 2 months, 65 grams; and at the incipient breeding age of 2½ months, 75 grams.

Once sexual maturity has been attained in the male there is no evidence of sterile periods or of sexual regression at old age, as there is in the female. Davis (1953) finds no evidence of testis regression in wild *Rattus norvegicus*. With one exception, where the testes were obviously abnormal, the testes of *R. a. assimilis* were actively producing sperm at the time of death. One wild-caught male sired a litter after 25 months in captivity.

The average life span of males born in captivity is 16 months. The record life span of two males bred in captivity is 41 months and of two wild-caught males is 39 months in the laboratory. There was no evidence from histological examination of the testes of sexual regression in any of these specimens. At this age, however, the animal is senile in appearance and activity and it is doubtful whether it would breed.

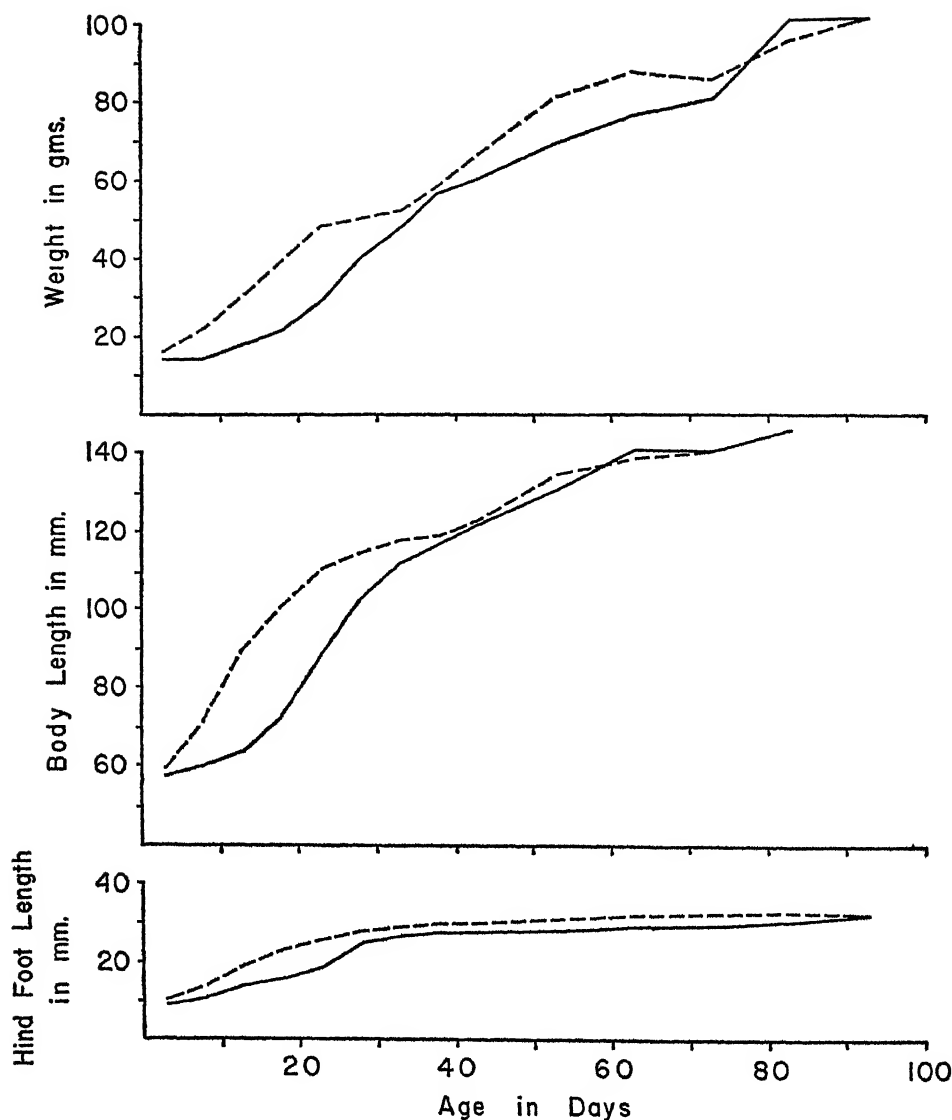


Fig. 10. Growth of *Rattus assimilis* in the laboratory. Solid line represents average growth curve of young of *assimilis* raised by *assimilis*; broken line, average growth curve of young *assimilis* raised by *Rattus norvegicus*.

Number of litters per female.—The mean number of litters per female is 3.6 for 34 females. Twelve of these females produced only one litter, and one female produced 14 litters in 15 months. The time span over which a female produced litters averaged 7.6 months. The longest span was 24 months. The greatest number of litters was produced by females that were either wild-caught or born early in the history of the colony. The mean figures derived from these laboratory colonies may be applicable to other laboratory colonies of this species. However,

little value can be attached to this information at present in interpreting the field situation. The same reservation, of course, pertains to the following discussion of reproductive rate.

Survival.—Working now from the averages obtained in the University of California colony, 3.6 litters per female and 38 young per litter, the average reproductive rate is 13.68 young per female. However, the number of young raised is the most important figure. The survival rate of the University of California colony is 81 young of 301 known to be produced, or 26.9 per cent, and of the Smith College colony 27 of 101, or 26.7 per cent. Thus the average survival rate of young per breeding female is 3.68 in the laboratory.

Attempts at cross-mating.—On four occasions a male of *Rattus assimilis assimilis* was caged with a breeding female of *R. norvegicus* in an attempt to crossbreed the two species. In two of these pairings the male was placed with its foster mother, and the other two pairings were of foster litter mates. No breeding or mating activity was ever witnessed, although the females were experiencing regular estrous cycles and the males were fertile.

GROWTH OF THE YOUNG

Limited data on growth of field-bred young have already been presented. Growth of the young of *Rattus assimilis assimilis* has been measured under laboratory conditions also. Growth in this rat is exceedingly variable under different conditions, and it appears to be a direct response to nutritive differences. Most young were raised by the female which bore them; in these animals both linear increment and weight gain followed the pattern shown in figure 10 and table 5. Although the sample measured is small, particularly in the pre-weaning days, the data in table 5 are enhanced by the fact that almost every day is represented by measurements of different rats. For instance, days 6–22 include 19 different individuals.

The pattern was one of fairly slow increment during the first 20 days and then, after the sampling of solid food, there was a 200–300 per cent acceleration in the average absolute growth rate from days 20–25 (table 6). The young of *Rattus assimilis* raised by the Long-Evans laboratory rat (*R. norvegicus*) increased in weight and size much more rapidly during the first 20 days, with a maximal absolute growth rate between days 10 and 15 (table 6). The gain under the latter conditions was more constant and did not attain the rate of acceleration of average absolute growth of young raised by *R. assimilis* (fig. 10 and table 7). Nevertheless, under both sets of conditions the young reached approximately the same end point at about the same time (Day 40). Individual variations among both groups of young after this age now become so diverse as to mask group differences. Only in hind-foot measurement did the young raised by laboratory rats continue to exceed the *assimilis*-raised young for several more weeks.

Average absolute growth rate, $R = \frac{W_2 - W_1}{t_2 - t_1}$, is used here as one interpretation.

Although this type of measurement is admittedly an abstraction only (Brody, 1945:504), it serves as a means of comparing two groups which do not show a logarithmic rate of growth and therefore are not mathematically eligible to

TABLE 5

GROWTH OF *RATTUS ASSIMILIS ASSIMILIS* RAISED BY *R. A. ASSIMILIS* IN THE LABORATORY

Days old	N	Weight: average and range (grams)	N	Body length: average and range (mm.)	N	Hind-foot length: average and range (mm.)
0.....	156	4.5 (2.5-6.0)	110	46 (38.9-51.4)	109	8.7 (7.0-10.0)
1.....	7	4.6 (3.9-5.6)	1	48	1	9.0
2.....	15	4.6 (3.6-5.1)	11	46.5 (41-53)	12	9.2 (8.9-8)
3.....	9	4.4 (3.7-5.4)	4	47.3 (45-51.1)	4	9.1 (9.0-9.2)
4.....	1	4.4	1	48	1	9.9
5.....	4	4.6 (4.3-4.8)	4	48.8 (46.7-51)	4	9.6 (9-10.2)
6.....	1	4.9	1	48	1	10.8
7.....	2	5.0 (4.6-5.4)	2	49.8 (46.5-53)	2	10.6 (10.5-10.7)
8.....	1	5.9	1	51.4	1	11.6
9.....	7	5.5 (3.9-7.1)	4	50.3 (48-51)	4	10.6 (10-11)
10.....	1	6.3	1	51.3	1	12.3
11.....	1	4.9	1	49	1	11.3
12.....	1	7.6	1	52.8	1	13.1
14.....	2	9.1 (9.1)	1	55	1	14.0
16.....	1	10.7	1	57.1	1	15.6
18.....	1	11.6	1	63.3	1	15.8
19.....	1	18.9
20.....	1	13.5	1	64.8	1	17.2
21.....	2	17.6 (16.2-18.9)
22.....	1	16.0	1	75.7	1	17.9
24.....	7	23.5 (18.2-26.2)	7	82.1 (74.8-86)	7	21.7 (19.1-27.0)
25.....	4	28.6 (26.8-29.7)	4	86.3 (81-90)	4	25.7 (25.0-26.5)
26.....	1	20.4	1	81	1	20.6
28.....	11	29.9 (22.0-40.8)	5	92.7 (82.6-103)	5	25.1 (21-27.9)
29.....	3	27.5 (23.5-34.3)
30.....	2	40.9 (39.6-42.1)	2	102.5 (95-110)	2	28.0 (27.1-28.9)
31.....	6	36.0 (33.6-41.2)	6	95.5 (92-102)	6	28.4 (27.0-29.2)
32.....	10	36.6 (25.0-44.3)	8	99.8 (88.5-105)	8	25.7 (22.6-27.8)
34.....	5	40.6 (30.9-42.5)	4	103.3 (96-100)	4	27.3 (25.9-28.6)
36.....	6	37.9 (26.2-43.4)	3	110.7 (105-115)	5	29.1 (26.1-32)
37.....	1	26.9	1	96.8	1	23.2
38.....	2	47.0 (45.7-48.2)	2	116	2	28.1 (28.0-28.1)
39.....	2	46.3 (36.0-56.6)	2	110 (98-122)	2	26.0 (24.4-27.5)
40.....	8	50.3 (41.1-69.4)	6	109.8 (97.7-123)	6	27.2 (23.3-29.5)
41.....	8	53.4 (39.7-62.2)	8	109.9 (104-120)	8	28.6 (24.8-30.7)
42.....	1	52.4	1	120	1	28.6
43.....	2	50.3 (42.0-58.5)	2	112.5 (108-117)	2	26.3 (25.2-27.3)
44.....	14	56.9 (33.3-68.2)	14	114.8 (97-128)	14	29.3 (24.5-31.2)
45.....	2	54.0 (43-64.1)	2	115.5 (110-121)	2	26.6 (25.3-27.9)
46.....	6	59.2 (49.4-70.5)	6	112.3 (99-123)	6	29.6 (28.1-30.9)
47.....	2	52.4 (45.0-59.7)	2	120.0 (113-127)	2	27.1 (25.9-28.3)
48.....	4	53.5 (49.1-60.3)	4	118.0 (106-125)	4	28.3 (26.0-31.3)
49.....	7	58.5 (48.4-63.6)	7	113.3 (103-122)	7	29.1 (26.5-30.7)
50.....	7	57.1 (49.3-65.8)	4	124.3 (115-133)	4	30.9 (30.0-31.9)
51.....	2	59.0 (49.3-68.7)	2	118.5 (115-122)	2	27.5 (26.3-28.7)
52.....	2	63.9 (58.8-69.0)	2	124.5 (123-126)	2	30.7 (30.4-31.0)
53.....	2	58.8 (49.9-67.7)	2	121.0 (112-130)	2	27.9 (26.6-29.1)
54.....	2	67.4 (63.2-71.6)	2	128.5 (125-132)	2	31.1 (30.2-32.0)

TABLE 5—Continued

Days old	N	Weight: average and range (grams)	N	Body length: average and range (mm.)	N	Hind-foot length: average and range (mm.)
55.....	2	61.3 (52.0-70.6)	2	118.5 (118-119)	2	28.0 (26.8-29.0)
56.....	2	68.3 (62.1-74.5)	2	133.5 (131-136)	2	30.6 (29.7-31.5)
57.....	2	63.7 (54.2-73.2)	2	123.0 (119-127)	2	28.1 (27.2-29.0)
58.....	2	72.2 (66.1-78.3)	2	126.0 (125-127)	2	31.1 (30.5-31.6)
59.....	2	64.5 (53.2-75.7)	2	125.5 (124-127)	2	28.6 (27.7-29.5)
61.....	2	64.4 (53.0-75.8)	2	128 (125-131)	2	28.5 (27.5-29.4)
62.....	2	74.3 (66.4-82.2)	2	131 (128-134)	2	31.9 (30.8-32.9)
63.....	2	66.6 (55.5-77.6)	2	131 (128-134)	2	29.0 (27.9-30.0)
64.....	4	71.3 (49.9-81.4)	4	123.8 (110-130)	4	30.2 (26.9-33.2)
65.....	2	70.4 (59.2-81.6)	2	130.5 (125-136)	2	29.0 (28.0-29.9)
66.....	3	72.3 (63.6-87.9)	3	114.3 (105-120)	3	28.0 (27.8-28.2)
67.....	2	69.6 (57.6-81.6)	2	125.0 (116-134)	2	28.9 (27.8-29.9)
69.....	4	75.3 (61.0-90.2)	4	129.5 (126-137)	4	30.6 (28.0-32.0)
73.....	2	69.7 (59.4-79.9)	2	131 (126-136)	2	29.3 (28.6-29.9)
76.....	3	77.2 (54.3-100.6)	3	130.3 (117-139)	3	30.9 (27.8-33.9)
80.....	3	69.8 (56.0-85.7)	3	131.0 (121-138)	3	28.9 (27.8-30.0)
83.....	3	90.0 (80.3-104.4)	3	137 (128-150)	3	31.8 (31.2-32.6)
87.....	2	83.6 (71.9-95.3)	2	136.5 (133-140)	2	29.6 (28.8-30.3)
90.....	2	99.4 (86.8-111.9)	2	145 (136-154)	2	32.8 (32-33.5)
94.....	2	84.3 (74.1-94.4)	2	137.0 (130-144)	2	29.5 (28.7-30.3)
97.....	2	100.9 (89.4-112.3)	2	145.5 (141-150)	2	32.8 (31.9-33.7)
101.....	2	87.3 (79.0-95.5)	2	138 (138)	2	30.3 (29.6-31.0)
104.....	2	104.2 (92.3-116.0)	2	154 (145-163)	2	32.9 (31.9-33.8)
108.....	2	91.3 (83.9-98.6)	2	137 (132-142)	2	30.2 (29.6-30.8)
111.....	2	105.1 (103.2-107)	2	154 (147-161)	2	32.8 (32.1-33.5)
115.....	1	90.5	1	145	1	30.8
122.....	1	92.2	1	140	1	31.1
125.....	2	111.0 (109-113)	2	132.5 (129-136)	2	29.8 (29.1-30.5)

be treated by the more realistic formula for instantaneous relative growth rate,

$k = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$. One might be misled by the average absolute growth-rate pro-

cedure: although the rate of the young raised by laboratory rats does not approach the magnitude of the *assimilis*-raised young, the peak acceleration of the former occurs at an earlier age and therefore may be more spectacular when compared with total body size at that time. For this reason it seems justifiable to treat the data by the instantaneous relative growth-rate method also, despite the fact that the data do not accurately follow a straight-line increment when plotted on a semilogarithmic scale. This is true both for plots of individual growth curves and for plots of the growth of collective samples.

Whereas with the average absolute growth-rate method all three dimensions measured showed a peak in rate at days 20-25 for *assimilis*-raised young and at days 10-15 for young raised by laboratory rats, the perspective is somewhat changed when the data are computed for instantaneous relative growth rates. The *assimilis*-raised young still show a peak rate at days 20-25 for all three

TABLE 6
AVERAGE ABSOLUTE GROWTH RATE OF *RATTUS ASSIMILIS ASSIMILIS*

Days old	Weight (grams)	Head and body length (mm.)	Hind-foot length (mm.)
RAISED BY <i>R. A. ASSIMILIS</i>			
0-5.....	.02	.56	.18
5-10.....	.34	.38	.32
10-15.....	.70	.98	.70
15-20.....	.74	1.84	.50
20-25.....	3.02	4.30	1.70
25-30.....	.88	3.24	.46
30-35.....	1.20	.90	.20
RAISED BY LABORATORY RATS			
0-5.....	.78	1.28	.74
5-10.....	1.26	2.72	.72
10-15.....	1.86	3.80	.94
15-20.....	1.60	1.72	.84
20-25.....	1.14	1.72	.30
25-30.....	.62	.56	.50
30-35.....	.38	.40	.12

dimensions (table 8). The young raised by laboratory rats, however, exhibit a maximum rate on days 10-15 in body-length increment only, and hind-foot and weight data show a general decline in rate from days 0-5 on.

These results are interpreted as meaning that the acceleration of growth during days 20-25 is normal for the *assimilis*-raised *assimilis* in the laboratory, and that it may be a direct response to a change to a solid food diet of much higher nutritive value than the milk of *R. assimilis*, which seems to be considerably less nutritive than the milk of the laboratory rat. The growth of young laboratory rats (*R. norvegicus*) was strikingly retarded when they were raised by *assimilis*. On Day 20, even after the young had been sampling solid food for several days, they were 40 per cent below normal weight and 10 per cent below normal body and hind-foot lengths.

The outstanding point in the growth pattern in the laboratory seems to be not so much that the growth rates differ under different conditions, but that the two groups actually reach the same end point within 40 days. The data for field-bred *Rattus assimilis* are different, however; the rate of growth is much more constant and the young grow more slowly. At 28 days of age the field-bred animals are from a few days to a week behind the *assimilis*-raised laboratory young in dimensions, the greatest disparity being in weight; and at 42 days of age the field-bred *assimilis* are about 10 days behind. The field-bred animals do not seem to be retarded in many of the developmental changes which accompany growth, such as the times at which ears and eyes open.

In the laboratory colony there is a suggestion of sexual differences in the

TABLE 7

GROWTH OF *RATTUS ASSIMILIS ASSIMILIS* RAISED BY *RATTUS NORVEGICUS* IN THE LABORATORY

Days old	N	Weight: average and range (grams)	N	Body length: average and range (mm.)	N	Hind-foot length: average and range (mm.)
3.....	5	5.8 (5.2-6.3)	5	49.1 (48.5-50.1)	5	10.3 (10.0-10.9)
4.....	5	7.0 (5.3-7.9)	5	50.4 (48.2-52.8)	5	10.9 (9.6-11.3)
5.....	5	8.4 (7.9-9.1)	5	52.4 (49.0-54.2)	5	12.2 (11.9-12.7)
7.....	5	10.8 (10.2-11.2)	5	60.9 (57.7-64.2)	5	13.5 (13.1-13.9)
9.....	5	13.8 (12.9-14.7)	5	63.8 (62.3-65.5)	5	15.4 (15.1-15.7)
11.....	5	17.4 (16.3-18.4)	5	72.9 (70.7-76.7)	5	17.0 (16.6-17.7)
13.....	5	20.6 (19.3-21.9)	5	80.6 (77.8-85.8)	5	18.9 (18.2-19.6)
16.....	5	26.8 (25.0-28.1)	5	88.4 (87-91)	5	22.0 (21.0-23.1)
18.....	5	28.9 (27.0-30.0)	5	90.8 (88-93)	5	23.5 (23.1-24.3)
20.....	5	32.1 (30.8-33.8)	5	93.6 (93-95)	5	24.7 (24.0-25.7)
21.....	1	42.3	1	98	1	26.2
22.....	9	38.8 (32.9-48.8)	9	100.4 (92-107)	9	26.2 (25.0-27.7)
24.....	5	36.9 (34.9-37.5)	5	101.4 (95-106)	5	26.0 (25.1-27.2)
26.....	6	40.0 (36.8-42.7)	6	103.5 (102-108)	6	26.8 (26.2-27.3)
28.....	9	40.5 (36.9-43.7)	9	104.8 (101-109)	9	28.1 (27.4-29.4)
30.....	1	47.8	1	104	1	28.7
34.....	1	52.4	1	110	1	29.2
35.....	4	42.7 (41.2-46.0)	4	107.3 (104-109)	4	29.3 (28.5-30.6)
38.....	1	58.3	1	108	1	30.4
42.....	5	57.1 (50.9-62.0)	5	110.8 (101-119)	5	29.9 (29.0-31.7)
46.....	2	56.0 (46.4-65.7)	1	122	1	29.3
49.....	4	65.5 (61.2-73.2)	4	118.8 (106-124)	4	30.9 (29.6-32.0)
50.....	1	68.2	1	126	1	30.8
54.....	1	73.0	1	125	1	31.8
55.....	5	81.2 (76.2-91.5)	5	128.4 (122-138)	5	32.8 (32.1-33.8)
56.....	4	67.7 (62.8-74.3)	4	125.3 (112-133)	4	32.0 (31.0-33.2)
58.....	1	74.3	1	126	1	32.1
63.....	4	77.3 (72.7-78.8)	4	128.8 (120-138)	4	32.0 (31.1-33.3)
70.....	5	81.0 (76.7-85.0)	5	136.8 (123-147)	5	32.2 (30.7-33.5)
71.....	1	70.2	1	130	1	33.6
77.....	1	88.5	1	135	1	32.1
84.....	1	86.5	1	136	1	33.1
90.....	1	83.0	1	136	1	32.5
105.....	1	100.2				

rate of growth of subadults. For *assimilis* young raised by *assimilis* these differences begin to appear at least by the age of six weeks; males then tend to exceed females in all the measurements taken: weight, body length, and hind-foot length (figs. 11, 12, 13). This differential growth pattern of the sexes does not clearly extend to young of *R. assimilis* raised by *R. norvegicus*. Here the growth pattern shows that weight and body-length increments of both sexes proceed at comparable rates (figs. 14, 15). Only the hind-foot length indicates that by the sixth week the rate of increment begins to accelerate faster for the male than for the female (fig. 16). It is not known whether there is a sexual difference in the growth rate of *R. assimilis* under natural conditions.

Some of the major changes in the development of *assimilis* young are illustrated

in figure 17 and plates 5 and 6. The measurements on the age chart (fig. 17) are meant as general indicators only. This chart applies specifically to the laboratory stock of *assimilis* which were raised by *assimilis*. It may be useful also as a guide to aging in the field, exclusive of the weights and measurements.

TABLE 8
INSTANTANEOUS RELATIVE GROWTH RATE OF *RATTUS ASSIMILIS ASSIMILIS*

Days old	Weight (grams)	Head and body length (mm.)	Hind-foot length (mm.)
RAISED BY R. A. ASSIMILIS			
0-5.....	.00437	.0051	.01978
5-10.....	.06279	.0033	.03082
10-15.....	.08832	.0080	.05428
15-20.....	.06394	.0133	.03128
20-25.....	.14996	.0249	.08027
25-30.....	.02852	.0149	.01725
30-35.....	.03335	.0037	.00690
RAISED BY LABORATORY RATS			
0-5.....	.12466	.02599	.07222
5-10.....	.11178	.04600	.05152
10-15.....	.09798	.05060	.05198
15-20.....	.05750	.01932	.03726
20-25.....	.03266	.01725	.01173
25-30.....	.01587	.00575	.01817
30-35.....	.00897	.00368	.00414

DISCUSSION

Despite the close relationship of *Rattus assimilis assimilis* to some of the most prolific mammalian breeders known to exist, both field and laboratory findings point to a relatively low reproductive capacity for this Australian species. Growth to sexual maturity occupies about one-quarter of the calculated average life span; the female produces on the average only a few litters in a lifetime, and litter size is small.

The relatively low density of populations of Australian mammals in many areas of the continent is perhaps more directly explained by the fact that many of the marsupials have only one or two young once a year. Yet here also is an Australian mammal, a rodent, which is reproductively capable of producing more young than can most marsupials, but which in no way begins to approach the reproductive level of some of its Eurasian and African relatives. What evidence is there to assist in explaining this situation?

Many parts of the Australian continent are deficient in soil micronutrients. The interests of sheep graziers account for much of the progress in the analysis of Australian soils. Some of the results have been spectacular. In an area in

South Australia which was deficient in copper and zinc, the land was capable of supporting only one sheep per 20 acres. When these trace elements were added, the sheep yield was increased to 40 sheep per 20 acres (Anderson and Underwood, 1959).

Pearl Beach, where *Rattus assimilis assimilis* was under investigation, is in an area which displays outcrops of Hawkesbury sandstone, and this locality lies

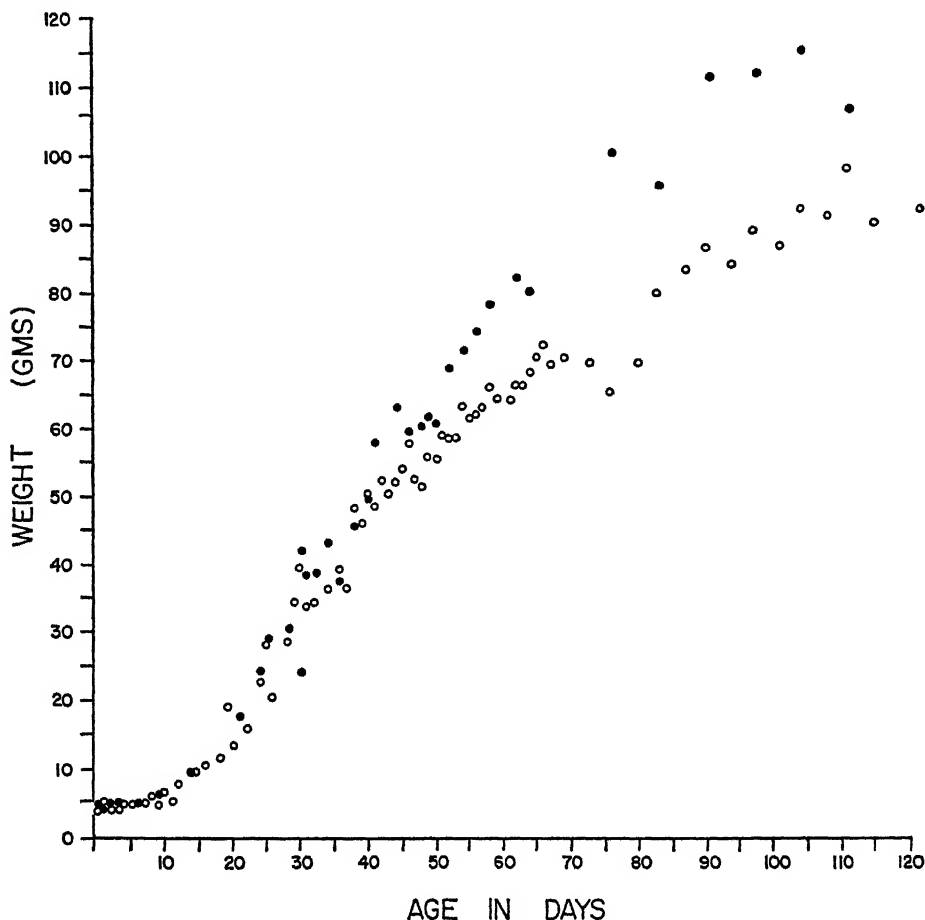


Fig. 11. Average daily weight of male and female *Rattus assimilis* young raised by *E. assimilis* in the laboratory. The open circles represent females; the solid circles, males.

within an extensive coastal strip deficient in soil phosphate and in molybdenum. Beadle (1954:374) tested oven-dried leaves of plant species native to the Hawkesbury sandstones and found a very low phosphate content, averaging less than 0.1 per cent. Molybdenum is a trace element important in nitrogen fixation and in the formation of certain animal proteins. Beadle (1953:427) states that "under Australian conditions, the elements required in the greatest quantity by the plants [fixed nitrogen and phosphate] are the first to become limiting." Beadle's results (1954:373) for the level of productivity of flax on the Hawkesbury sandstone

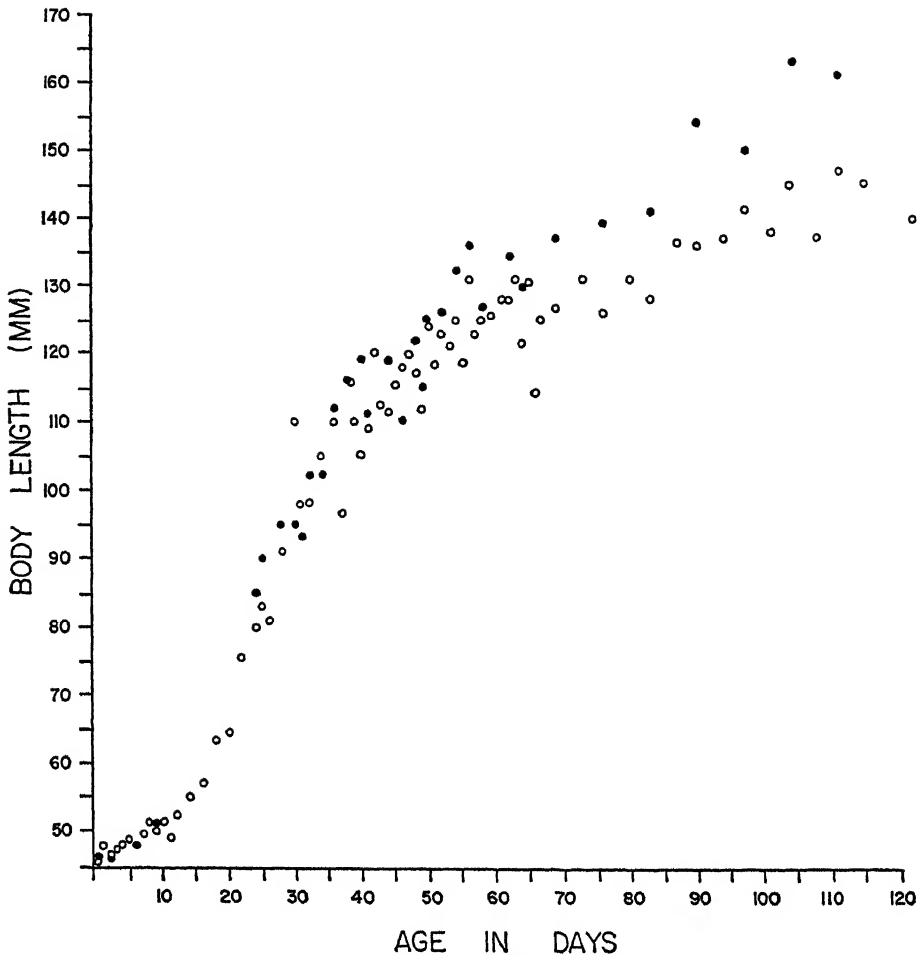


Fig. 12. Average daily body length of male and female *Rattus assimilis* young raised by *R. assimilis* in the laboratory. Same symbols as in fig. 11.

soils from Hornsby (about 14 miles from Pearl Beach) are as follows: on the control soil, 23 ± 5.2 mg.; with NO_3 added, 31 ± 5.0 mg.; and with P_2O_4 added, 82 ± 1.4 mg. The low nutrient level of these sandstone soils, according to Beadle (1953), seems to account for the lack of native annual species of plants in this area. If indeed the nutrient level is too low to support the life cycle of an annual plant, may not this situation be reflected also in the faunal components of the area?

There are no reports of population outbreaks of *Rattus assimilis assimilis* in this native habitat. If there were outbreaks and the rodent thus seriously depleted the vegetation, the plants with their low productivity rate would take years rather than months to recover. It seems advantageous, then, for *R. a. assimilis* to remain at a constant density level and at a low density level in order to exploit this type of habitat without depleting it.

In *Rattus assimilis assimilis* the reproductive rate appears to be genetically

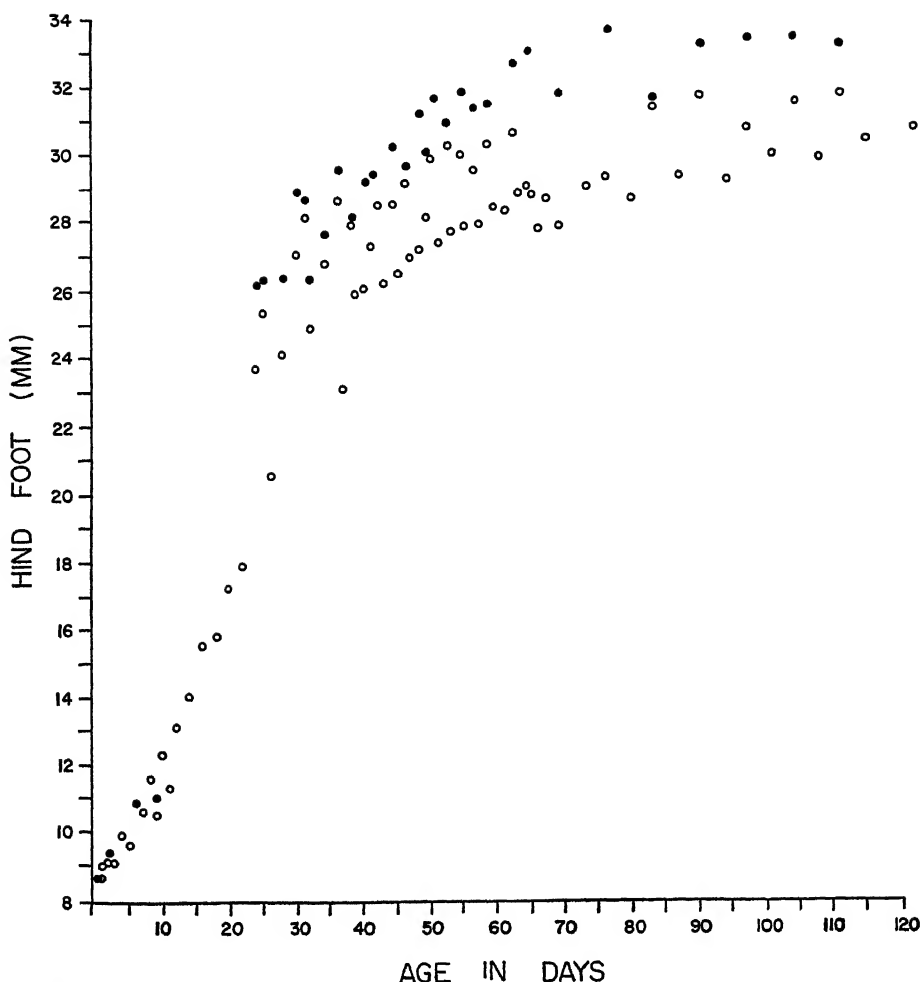


Fig. 13. Average daily hind-foot length of male and female *Rattus assimilis* young raised by *E. assimilis* in the laboratory. Same symbols as in fig. 11.

determined and not a direct response to nutritional conditions. If it were the latter, one would expect an increase in the reproductive rate in response to a nutritious laboratory diet. Selection has probably operated against the survival of large litters and has favored the perpetuation of animals bearing genetic factors that result in small litters. This mode of reproduction may then be a means of maintaining a constantly low population level and thus of exploiting to a maximum this nutrient-deficient habitat.

SUMMARY

Field evidence suggests that the population of *Rattus assimilis* is generally sparse in its native habitat in Australia. Sixty-five individuals were captured a total of 182 times in 7,900 trap nights on a 22-acre tract of coastal *Eucalyptus* forest.

Habitat favoring the establishment of burrow systems appears to be important in the local occurrence of this rodent.

Age categories have been worked out for field-caught specimens. The utilization of this method in addition to evidence of lactation and pregnancy in field animals and on museum specimens leads to the conclusion that breeding occurs throughout the year in the field. The litter size under field conditions ranges from 3 to 6. The sex ratio of adults in the field is approximately 50:50. The normal life

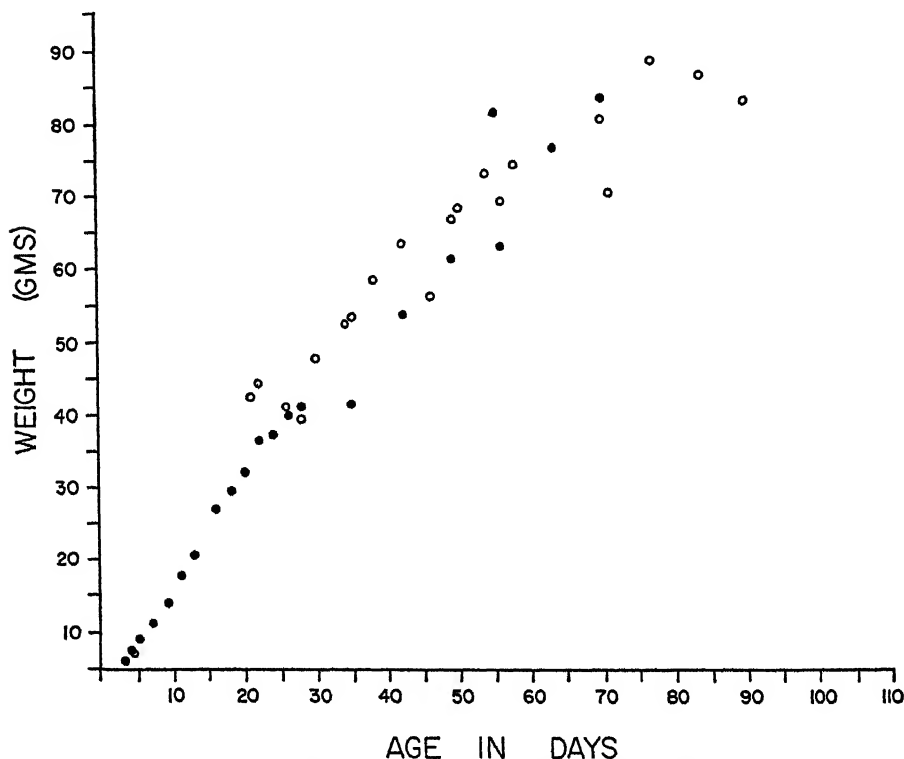


Fig. 14. Average daily weight of male and female *Rattus assimilis* young raised by *R. norvegicus*. Same symbols as in fig. 11.

expectancy of rats that reach the weaning stage is estimated not to exceed a year.

Habitat and growth comparisons are made with the introduced *Rattus rattus* of the area. *Rattus rattus* does not seem to have the same habitat preference as *R. assimilis* and is not regarded as a competitor of this native species. The two species have the same general range of adult weights, but *R. assimilis* is slower in rate of growth and development.

The gross anatomy of the reproductive system of *Rattus assimilis* is very similar to that of *R. norvegicus*. The most conspicuous differences are in external genitalia.

The estrous cycle of *Rattus assimilis* averages 4.5 days. Histological changes in the ovary, uterus, and vagina follow closely those reported for *R. norvegicus*. The average number of corpora lutea formed per ovulation is 7. The

female experiences a postpartum estrus on the average 1.7 days after parturition, and a lactation anestrus lasting 20–24 days after postpartum estrus. Nonlactation anestrus lasting 10–44 days is experienced in the laboratory. Pseudopregnancy can be induced with electrical stimulation and lasts 15–17 days. A sterile cycle between the time of vaginal perforation and regular estrous cycles is experienced by young rats in the laboratory.

The average gestation period is 22.8 days and ranges from 22 days to 24 days.

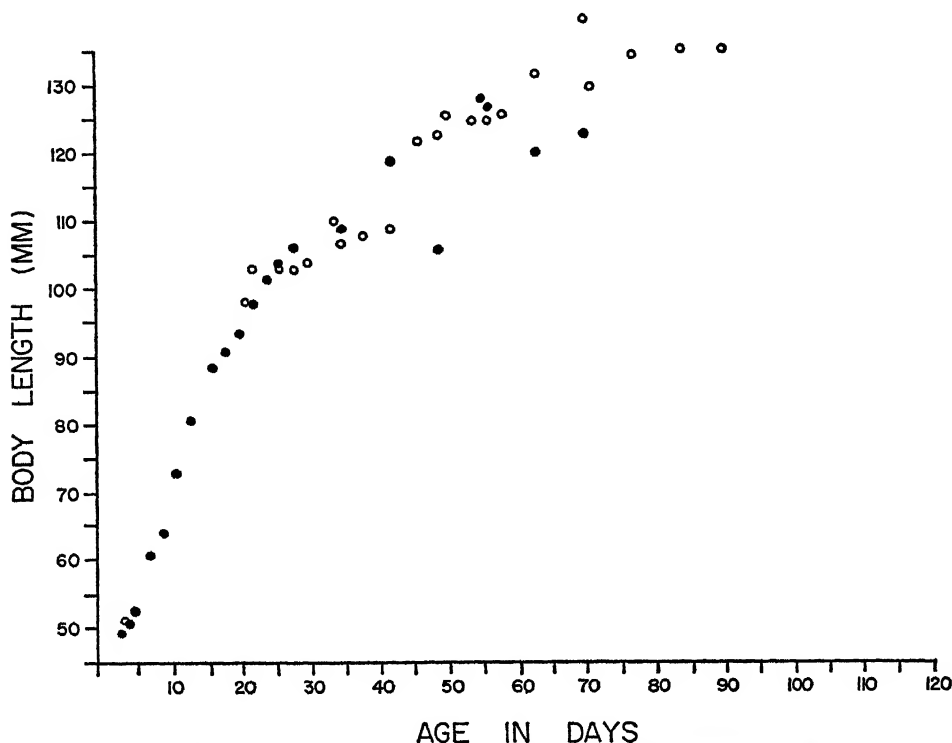


Fig. 15. Average daily body length of male and female *Rattus assimilis* young raised by *R. norvegicus*. Same symbols as in fig. 11.

Gestation while the female is lactating lasts 28–32 days; delayed implantation may be responsible for this increased duration. Of the time-recorded parturitions, 80 per cent occurred between 2 P.M. and 8 P.M.

The sex ratio of young is approximately 50:50. The number of young per litter ranges from 1 to 7, averaging 3.81 in the colony maintained at the University of California and 4.21 for a colony at Smith College. The mode is 4. Prenatal loss is about 40 per cent. The mean number of litters per female is 3.6 in the laboratory. Litters are produced on the average over a span of 7.6 months. The average survival rate of young per breeding female in the laboratory is 3.68. Weaning occurs during the latter part of the fourth week after birth.

Breeding occurs throughout the year in the laboratory.

The vagina opens on the average on the 46th day. The average age at which

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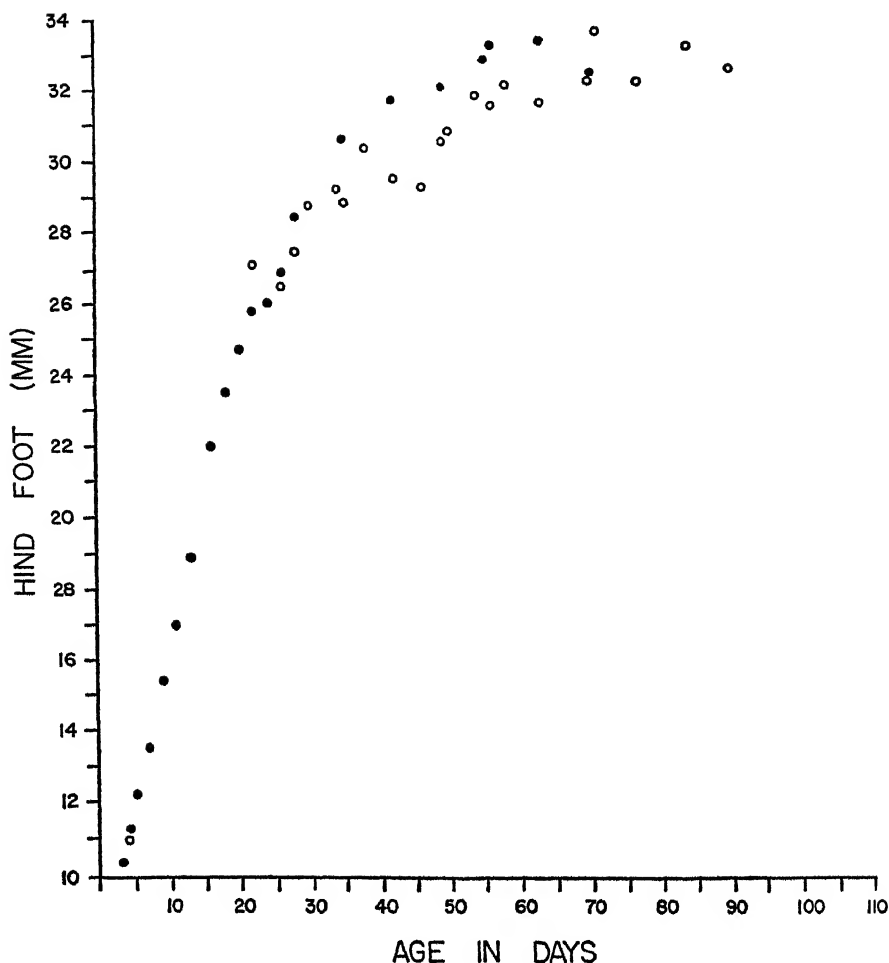


Fig. 16. Average daily hind-foot length of male and female *Rattus assimilis* young raised by *R. norvegicus*. Same symbols as in fig. 11.

females breed in the laboratory is $4\frac{1}{2}$ months, and the average age at which a female ceases to produce young is 12 months.

The mean life span of both males and females in captivity is 16 months.

Male *Rattus assimilis assimilis* begin to produce spermatozoa at the age of $2\frac{1}{2}$ months, but usually do not breed before the age of 4 months. There is no evidence of sterile periods or sexual regression at old age in the male. The male appears to be continuously fertile throughout the year.

Attempts to breed *Rattus assimilis* with *R. norvegicus* were unsuccessful.

The growth rates of young of *Rattus assimilis* raised by *assimilis* and of young of *assimilis* raised by *norvegicus* differ, although by the 40th day the two groups of young are about equal in weight and size.

Rattus assimilis is similar to *R. norvegicus* in length of estrous cycle and ges-

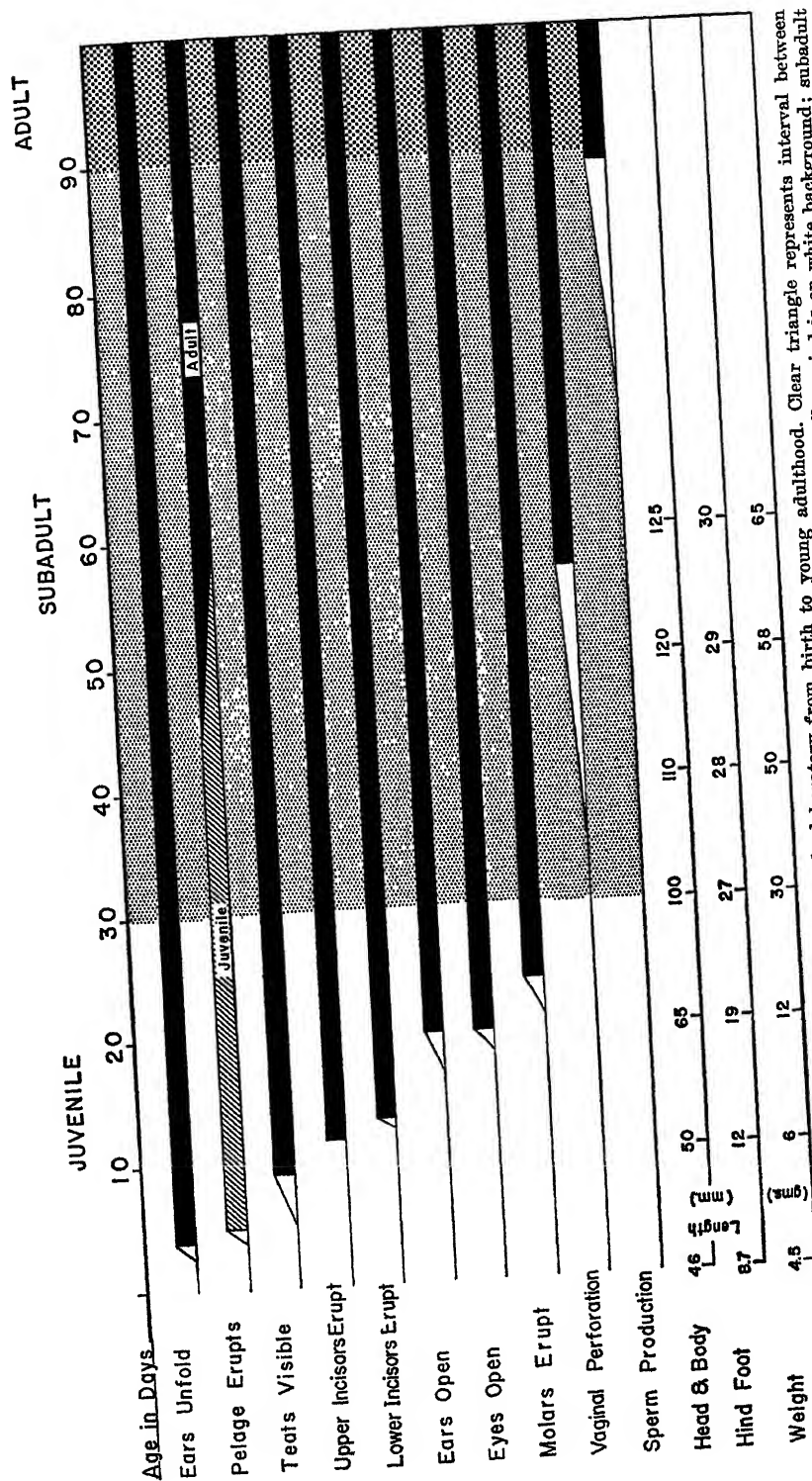


Fig. 17. Stages in the development of *Rattus assimilis* in the laboratory from birth to young adulthood. Clear triangle represents interval between minimum and maximum times at which event occurred. Juvenile pelage represented by hatched lines. Juvenile period is on white background; subadult period, on stippled background; adult period, on heavily stippled background.

tation period, time of implantation, lactation anestrus, and percentage of intra-uterine loss. *Rattus assimilis* differs conspicuously from *R. norvegicus* in the smaller number of corpora lutea per estrous cycle, the delayed time of postpartum estrus, the greater length of lactation, the smaller number of young per litter, the smaller number of litters per female, the slower rate of growth and development, and the reduced mammary formula.

It is suggested that the low reproductive rate and the year-round breeding of *Rattus assimilis assimilis* may be of long-term selective advantage as a method of maintaining a constant and low population level—a level which in turn enables the species to exploit to the maximum a habitat deficient in certain micronutrients.

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PLATES



East view from Warrenton, Oregon, showing the town of Portland and the Pacific Ocean
Photograph taken March 26, 1900 by J. Van Dusen



a Warruk Sanctuary in coastal *Podagraceae* forest. The distant view was typical of the 22 acre segment by-trapped for *Tathys assm* by. Photographed in March 1955 by J. Mary Taylor



b Low scrub forest on an east facing slope of Warruk Sanctuary. Part of a sandstone outcrop is shown in the immediate foreground. Broken Bay and Box Hill are in the distance. Photograph (Kodachrome) taken April 3, 1955, by B. Elizabeth Horner



a Ovary of minute *Pteromalus assimilis* one month old showing primary and growing follicles $\times 22$



b Ovary of minute *Pteromalus assimilis* with three fully formed corpora lutea $\times 22$



a. Semiferous tubules from the testis of a mature *T. a. assimilis*. The tubule walls are near the center of the photograph and the spermatozoa and lumens are near the top and bottom. $\times 600$.



b. Semiferous tubules from the testis of a mature *T. a. assimilis*. The tubule walls are near the center of the photograph and the spermatozoa and lumens are near the top and bottom. $\times 600$.



a Laboratory reared *Rattus assimilis* male 7 days old 134



b Laboratory reared *Rattus assimilis* female 21 days old 134



a. Laboratory-raised *Rattus assimilis assimilis*, female 28 days old. $\times \frac{3}{4}$.



b. Laboratory-raised *R. a. assimilis*, female adult. $\times \frac{3}{4}$.

VARIATION IN SOME
SALT-MARSH POPULATIONS OF
MICROTUS CALIFORNICUS

BY

CHARLES S. THAELE, JR.

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VARIATION IN SOME SALT-MARSH POPULATIONS OF *MICROTUS CALIFORNICUS*

BY

CHARLES S. THAELE, JR.

(A contribution from the Museum of Vertebrate Zoölogy of the University of California)

INTRODUCTION

IT HAS long been known that the voles of the salt marshes around San Francisco Bay differ from those in the surrounding upland localities (Grinnell, 1913). Kellogg (1918) proposed the name *Microtus californicus aestuarinus* for the rather large dark form of these mice found in the Central Valley of California and in the marshes on the north side of Suisun and San Pablo bays. He also suggested that the mice from marshes around the south end of San Francisco Bay might be distinct from *M. c. californicus*. In 1935 Hatfield assigned the name *M. c. paludicola* to the mice occurring in salt marshes from El Cerrito, Contra Costa County, south around the southern arm of San Francisco Bay. In his summary of rodents of the Bay Area, Hooper (1944) extended the range of *M. c. aestuarinus* by recognizing the voles from the south side of Suisun Bay (i.e., the salt marshes east of Martinez) as *M. c. aestuarinus* and those from the marshes at Giant and the mouth of San Pablo Creek as intermediate in characters between *M. c. aestuarinus* and *M. c. paludicola*, although he assigned them to the former subspecies.

ACKNOWLEDGMENTS

I acknowledge with thanks the assistance, suggestions, and criticisms of those who have aided and encouraged me in this study. First I wish to express my sincere gratitude to Dr. Seth B. Benson, who not only suggested the problem to me but remained a continuing source of guidance and criticism, thereby contributing much to the preparation of this monograph. I am indebted also to Dr. Chin Long Chiang and Dr. William F. Taylor, who suggested the methods used in the statistical analysis of the data, and to Dr. Taylor and Dr. Alden H. Miller for their criticism of the manuscript. I am grateful to Mr. George Fisler and Mr. Alan C. Ziegler for help in collecting specimens, to Mr. Elbert M. Brock for allowing me to examine some vole skulls of known age, and to Dr. William Z. Lidicker, Mr. George Fisler, and Mr. Ned Johnson, with whom I discussed this work and whose comments have proved most valuable. Finally, my thanks to Mr. Gene Christman for assistance in the production of the figures.

POPULATIONS TREATED

Samples from ten different localities were used in this study (see fig. 1). These will be referred to as (1) Berkeley Hills (B.H.)—various localities within one mile of Strawberry Canyon in Alameda and Contra Costa counties; (2) Grizzly Island (G.Is.)—located on the north side of Suisun Bay, Solano County; (3)

Tracy Lake (Tr.L.)—6 miles SW Galt, San Joaquin County; (4) Walnut Creek (W.Cr.)—various localities between Lafayette and Mount Diablo, Contra Costa County; (5) Pinole (Pin.)—a salt marsh 0.7 mile N, 0.2 mile W Pinole, Contra Costa County; (6) Martinez (Mart.)—several localities in salt marshes east of Martinez including a series from 1 mile W Avon; (7) San Pablo Creek (S.P.Cr.)—salt marshes at the mouth of San Pablo Creek and also W Giant, Contra Costa County; (8) Point Isabel (Pt.I.)—salt marshes 0.5 mile W El Cerrito, Contra

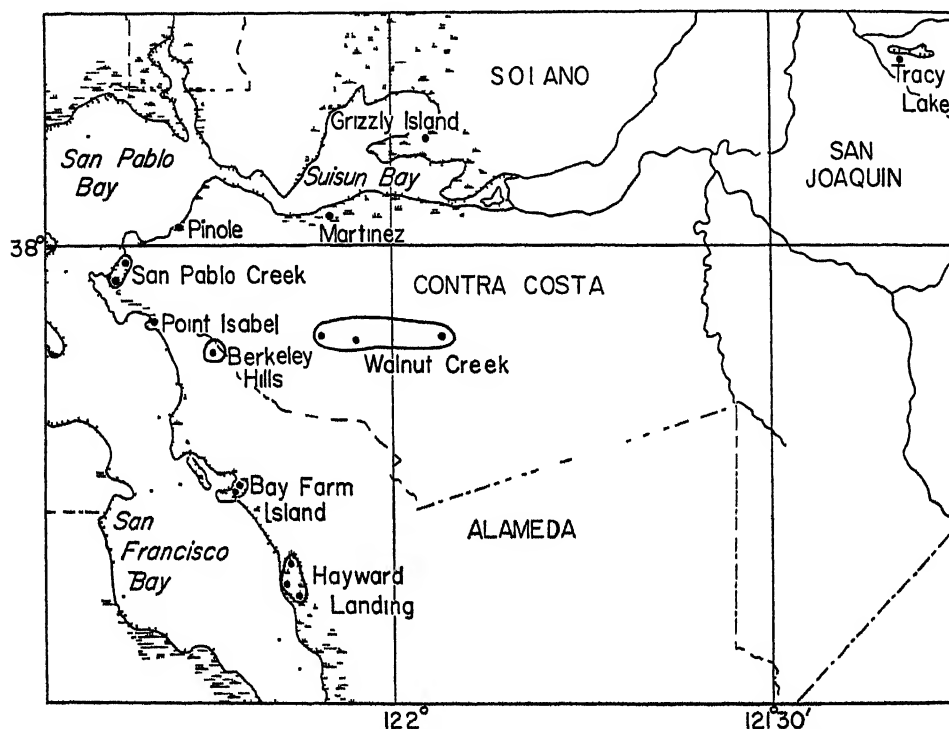


Fig. 1. Map of San Francisco Bay area showing localities included in this study and the distribution of salt marshes.

Costa County, and along the Eastshore Freeway, Alameda County; (9) Bay Farm Island (B.F.Is.)—various localities within a half-mile radius, including specimens from Melrose Marsh, all in the salt marshes near Bay Farm Island, Alameda County; and (10) Hayward Landing (H.L.)—three localities in the salt marshes including specimens from Alvarado and a point $5\frac{1}{2}$ miles S San Leandro, all in Alameda County. Specimens from more than a single locality have been lumped together only when the intervening area does not represent an obvious natural barrier. Therefore, each sample may be considered as having been drawn from a single population.

The material used in this study is in the Museum of Vertebrate Zoölogy (abbreviated MVZ) of the University of California. Several series, notably those from Martinez and San Pablo Creek marshes, have recently been augmented by specimens collected by the author and others.

METHODS

AGING

Several features of the development, life history, and morphology of *Microtus* complicate taxonomic studies of this group. The life expectancy of the animal is very short relative to its period of growth. Blair (1948) estimated the average life span for *M. pennsylvanicus* to be 4.23 months, but many individuals continue to grow after they have reached this age. Fitch (1957) states that for *M. ochrogaster*, animals measuring 160 mm. (total length), which are about five months old, the growth rate is about 0.1 mm. per day. As a consequence, wild-caught samples of voles show, for most measurements, wide variations resulting from the age differences within the sample. In his recent study of *M. montanus* Anderson (1959) also has made this point. Since *M. californicus* is reproductively mature at least by two months of age (Greenwald, 1957), and since it completes its molt into adult pelage at about this time (Ecke and Kinney, 1956), the criteria of molt and reproductive maturity cannot be used to eliminate variation in measurements resulting from age differences. Significant differences were found in a series of measurements from two samples of voles, all with adult pelage. These series came from different localities within one mile of each other in the Berkeley Hills. Difference in the average age of the samples accounts for the apparent size difference between these two samples.

It is necessary, then, to find some criteria that can be used to group individuals of the same age so that comparisons can be made. Although the degree of tooth wear has been used for this purpose in some mammals, the ever-growing nature of *Microtus* teeth precludes this possibility. Howell (1924) has pointed out the difficulty of using the degree of suture closure in *M. montanus* as a criterion of age. Although various authors have used weight, total length, and length of skull as bases for estimating the age of voles, such criteria do not give comparable groups when populations of different size are compared.

This view differs somewhat from that expressed by Anderson (1959) in his work with *Microtus montanus*. He used an arbitrary lower limit of body length or condylobasilar length to distinguish adult animals. He argued that such a procedure would introduce less bias than the use of other "more subjective" criteria. However, he attempted to compensate for age variation in condylobasilar measurements by the use of his "index of maturity" when comparing this measurement among various populations. This correction may be considered similar to the corrections made for all measurements affected by age variation shown here in tables 1-3 and figures 4-17.

In this study I have adopted a method devised by Snyder (1954), in his study of *Microtus pennsylvanicus*, for obtaining an age index. The method is based on changes in appearance, correlated with increasing age, of three regions of the posterior portion of the skull: the exoccipital-mastoid crest, the lambdoidal crest, and the paroccipital processes. Numbers were assigned to four arbitrarily designated stages in development of these regions. (Snyder recognized only three stages of development of the paroccipital processes in *M. pennsylvanicus*.) The sum of these three numbers for each skull gives an age index consisting of ten classes

(3-12). In practice there was rarely a difference of more than one between any two values assigned to these regions of a given skull, although the stage of development for each character was judged independently. Also, when a sample was divided into classes, the averages of most measurements for each successive class showed a progressive increase. These classes are not to be considered comparable to those of Snyder, nor do the classes represent equal time intervals.

This age index is admittedly subjective and not entirely reproducible. Although the series of skulls first grouped into classes (Berkeley Hills) was used as a basis for all future work, repeated classification showed that the results could not be reproduced exactly. However, the differences appeared to be slight. How accurate this method is in establishing true age classes is not known. The comparison between the estimated age class and the known age of a few skulls is discussed below.

STATISTICAL ANALYSIS

It is not feasible to compare only specimens of a single class or even to combine two successive classes, since the sample size would then be too small. For example, a large series from the Berkeley Hills (91 specimens) was found to contain only 18 animals of both sexes from the two oldest classes. Although Snyder felt he could combine the four oldest groups in his work with *Microtus pennsylvanicus*, the criteria he used in establishing age groups may have resulted in a somewhat different composition of these categories. Therefore comparisons were made by an analysis of covariance. This eliminated any errors that might result from combining several classes. Furthermore all the available data could be used.

In performing an analysis of covariance the following procedure was applied. First, a test was made to determine whether the measurement increased with age (i.e., test of the hypothesis $\beta = 0$). β refers to the slope of the regression of a given measurement on the age index. A second test was performed to determine whether the increase with age, if present, was the same for each population (i.e., test of the hypothesis $\beta_1 = \beta_2 = \dots = \beta_k$). If neither of these hypotheses was rejected, a test was then performed to see if the populations were the same (i.e., to test the hypothesis that a single regression line could be used for all the samples). The procedure for these analyses is that outlined by Wilks (1948). Finally, following the procedure suggested in Dixon and Massey (1957), a test was made to determine whether the relation between size and age was linear. All tests were judged at the 5 per cent level of significance.

The skulls which fell into classes 3, 4, and 5 were from obviously young animals, and none of these classes were well represented in the sample. The specimens in age class 6 and older were in adult pelage and those in younger classes had not yet obtained a full adult pelage. Therefore, only specimens of class 6 and above were used in these analyses.

The following series of skull measurements were made: greatest length of skull, condylozygomatic length, length of diastema, length of rostrum, cranial breadth, cranial height, interorbital breadth, zygomatic breadth, and length of molar row. The first eight of these were measured as described by Snyder (1954). The length of molar row was measured along the occluding surface of the upper molars. The

standard body measurements (total length, tail, and hind foot) were those of the collector as recorded on the specimen labels.

COLOR ANALYSIS

In most taxonomic studies the pelage color of specimens is of importance. However, the nature and extent of variation in color must be recognized before any conclusions can be drawn about the differences in color between populations. Various authors (Durham, 1941; Anderson, 1956; Rudd, 1955; Bowers, 1956; and Norris, 1958, to mention a few) have used different methods to achieve this aim. In this study the Munsell Color Charts (1942) were used as the color standards. R. S. Miller (1958) and Bowers (1956) have discussed the advantages of this system of color notation.

A group of specimens was selected to match the color chips representing the variation shown by the mid-dorsal pelage of the specimens to be analyzed. Using these skins as standards, the remaining skins were matched with this series. This procedure was adopted because the individual hairs differ in color and the resultant blended color was the one that was to be determined. Where skins represented intermediate colors, interpolations were made. Matching of colors was done under constant daylight conditions.

Since the variation in chroma was slight and tended to parallel the variation in value, I felt that the former variable (chroma) could be omitted without introducing serious error. This modification in the color designation allowed the construction of scatter diagrams on which to base comparisons of various samples. Hue and value were plotted on the horizontal and vertical axes, respectively (figs. 2, 18, 19, 21).

ANALYSIS OF NONMEASURABLE DIFFERENCES

Comparisons of nonmeasurable differences in skull structure and teeth were made between specimens representing the same sex and class. These differences have been mentioned where at least 75 per cent of the specimens of each subspecies could be identified correctly on the basis of the character being considered. Such characters include shape of the zygomatic arches, shape of the auditory bullae, and shape of the brain case.

INTRAPOPULATION VARIATION

An intensive study was made of the variation within a single population. For this study a sample of 91 specimens from the Berkeley Hills was used. Analysis of the measurements revealed that, of the three body measurements and nine skull measurements taken, all but those of the hind foot and interorbital breadth varied significantly with age. Furthermore, of those which did vary with age there was no significant difference between males and females. When a *t*-test ($\alpha = .05$) was applied to the measurements of the hind foot and interorbital constriction a significant difference was found between males and females (see table 3).

Using these conclusions, a pattern was established for comparing samples from the ten localities noted earlier. All measurements except those of hind foot and

interorbital breadth were compared by an analysis of covariance, and the sexes were not separated. Measurements of hind foot and interorbital constriction were compared by an analysis of variance, and sexes were considered separately.

A study of intrapopulational color variation was made, using the scatter diagrams previously described. Using a large sample collected at one time (i.e., part of S.P.Cr. sample), the colors of individuals, all class 6 or above, were plotted and designations of age and sex were included for points on the scatter diagram.

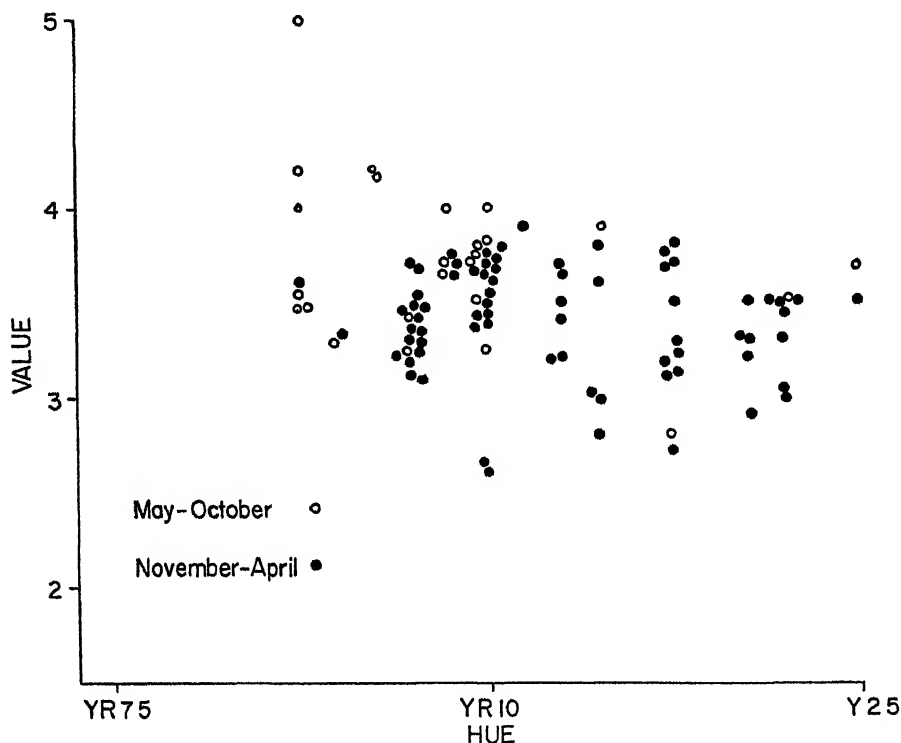


Fig. 2. Scatter diagram showing seasonal difference in dorsal pelage color of Berkeley Hills sample, class 6 and above.

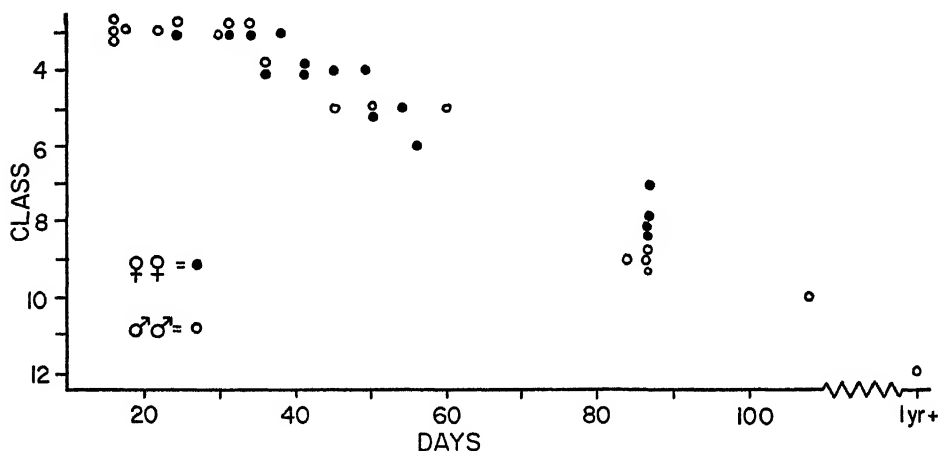
However, color variation did not appear to be related to either sex or age. Then the colors of individuals of another large sample (B.II. sample) were plotted, with the month of collection designated. This showed a decided dichotomy in color of the sample. Specimens collected from November through April were darker and more yellow than specimens taken throughout the remainder of the year (fig. 2). The latter were lighter and more reddish. There was a narrow zone of overlap between the colors for these two parts of the year. Aside from this overlap, only 6 per cent (5 in 84) of the individuals were inconsistent.

Further investigation of the remaining samples showed that such a distinction was apparent in all samples which included specimens from both periods of the year, with the exception of the sample from Martinez. Thus in comparing samples only specimens collected between November and April were used.

CLASSES OF KNOWN-AGE SKULLS

Through the kindness of Elbert M. Brock and Alan C. Ziegler I was able to study 36 known-age skulls of *Microtus californicus* which had been raised under a variety of laboratory conditions. I was interested in determining whether the results obtained from the scheme for estimating age employed here were reasonably consistent with the known age of these specimens. Figure 3 shows the comparison between age index and known age. Animals in class 6 are about 55 days old and have adult pelage, which is consistent with the findings of Eecke and Kinney (1956) that *M. californicus* starts its molt into adult pelage at about 50 days.

Furthermore, it can be seen that females about 85 days old were placed in a



populations of voles, these factors will be briefly described. On the south side of Suisun Bay, marshes extend from a point 5 miles west of Antioch to the vicinity of Martinez. It is possible that these marshes once extended farther east, but apparently never east of Antioch, since here the bay is bordered by a stretch of high ground. These marshes formerly covered about 7,000 acres, but their present expanse is 5,000 acres or less. The marshes on the north side of the bay cover about 50,000 acres and are connected with extensive marshes in the delta.

To the west, the highlands bordering the Carquinez Strait preclude the possibility of any habitable belt of marsh. From the Strait to Giant several unconnected marshes occur at the mouths of small streams. These are of limited extent. The marsh at Pinole covers about 30 acres. South of Giant there formerly was an almost continuous belt of marsh to a point beyond Point Isabel. However, within the past seventy years much of the area has been altered; this marsh is now separated into two major parts: the northern part includes the marshes from Giant south to San Pablo Creek; the southern part includes Point Isabel and several small marshes south of Richmond. The more northern part once had an area of about 2,500 acres, which has been reduced to 1,000 acres. The marsh at Point Isabel has decreased from 250 to 75 acres.

South of Point Isabel no marshes are shown on maps of the 1890's. The possibility that any extensive marshes existed earlier is precluded by the topography of the area. The 25-foot contour line (USGS quadrangle, San Francisco, ed. 1899, surveyed 1892-1894) comes within less than a tenth of a mile of the bay. Only a narrow band of marsh habitat could have been present in the area. Farther south, marshes seem to have been relatively continuous around the southern end of the bay, covering about 60,000 acres, but at present the area is somewhat less.

The descriptions are based on United States Geological Survey quadrangles (Antioch 1908 ed.; Palo Alto, 1899 ed.; San Francisco, 1899 ed.; San Jose, 1899 ed.; San Mateo, 1915 ed.). The scale of each is 1:62500. The figures indicating acreage are rough approximations intended to illustrate the relative differences. Some estimates of the present extent of these marshes have been made from personal observations.

RESULTS OF THE COMPARISONS OF POPULATIONS

All twelve measurements used in this study were found to vary significantly among the ten populations studied. For the ten measurements that varied significantly with age, the hypothesis that a single regression line could be used to represent all ten populations was rejected; for the two measurements that were independent of age, for animals in class 6 and above, the hypothesis that the mean was the same for all ten populations was rejected. Therefore, it is of interest to determine which differences between populations are significant, that is, which differences led to the rejection of the hypothesis of a single regression line or of equal means. A method developed by Scheffé (1953, 1959) for judging all possible contrasts between pairs or groups of populations was employed. First, the differences between various pairs of populations were tested for significance. When a significant difference was found between any two populations it was assumed that all pairs involving

more extreme combinations were also different. Following the suggestion of Scheffé (1959), all contrasts were tested at the 10 per cent level of significance.

The results of these contrasts are summarized in figures 4-17. For the estimate of the mean of each population at class 9, shown on tables 1 and 2 and figures 4-17, the estimate of the common slope, B_w , was used. Following a procedure suggested by Duncan (1955), these means have been plotted and lines drawn under them: all means underscored by a given line were found not to differ significantly from one another, and all means not underscored by the same line did differ significantly.

Since several of the available samples were small (less than 25), contrasts including such samples were not very discriminatory, and differences that might be recognized with larger samples are not distinguished. Hence additional contrasts were made between groups of populations: two or more populations on one hand and one or more populations on the other. The groups tested were those suggested by the data. For example, when the tail length of mice from the Berkeley Hills is contrasted with that of mice from any one of the three populations assigned to *Microtus californicus paludicola* by Hatfield (H.L., B.F.Is., or Pt.I.), no significant difference is shown (fig. 5). However, if the three *M. c. paludicola* samples are grouped together, tail length in this group is found to be significantly shorter than in the Berkeley Hills population. A summary of such contrasts follows.

In total length (fig. 4), the Grizzly Island and Tracy Lake group was found to be longer than the Martinez population. The Walnut Creek, San Pablo Creek, Pinole, Berkeley Hills, Hayward Landing, and Bay Farm Island group is shorter than the Martinez population. The Point Isabel population is shorter than the group of six localities listed.

When tail measurements for Bay Farm Island, Hayward Landing, and Point Isabel are grouped, they are shorter than those of the Berkeley Hills population (fig. 5).

The hind-foot length of males (fig. 6) in the Tracy Lake and Grizzly Island group was not significantly longer than in the Pinole population. The latter was not significantly longer than in the Hayward Landing, Martinez, Berkeley Hills, San Pablo Creek, Walnut Creek, and Point Isabel group, and this group was not significantly longer than in the Bay Farm Island population.

When the hind-foot length of females (fig. 7) in the Grizzly Island and Tracy Lake group was tested against the Martinez population, the latter was significantly shorter, but the former two were not shorter than the Pinole population. The Martinez population was found to be longer than the Hayward Landing, Walnut Creek, Berkeley Hills, San Pablo Creek, and Point Isabel group. The latter group was longer than the Bay Farm Island population.

When the greatest length of skull of the Martinez population was tested against all shorter populations (fig. 8), it was found to be significantly longer.

In zygomatic breadth (fig. 9) the Tracy Lake and Grizzly Island group was wider than the Martinez population, but not wider than the Pinole population. The Martinez population was found to be not wider than the San Pablo Creek, Bay Farm Island, Walnut Creek, Hayward Landing, and Berkeley Hills group.

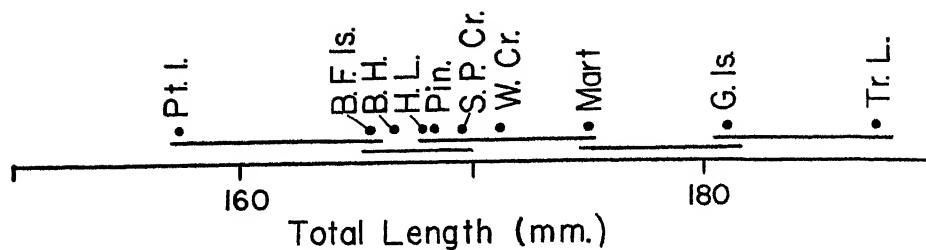


Fig. 4. Summary of contrasts of pairs of populations for total length. All populations above a single line are not significantly different from one another. Abbreviations as on pp. 67 and 68.

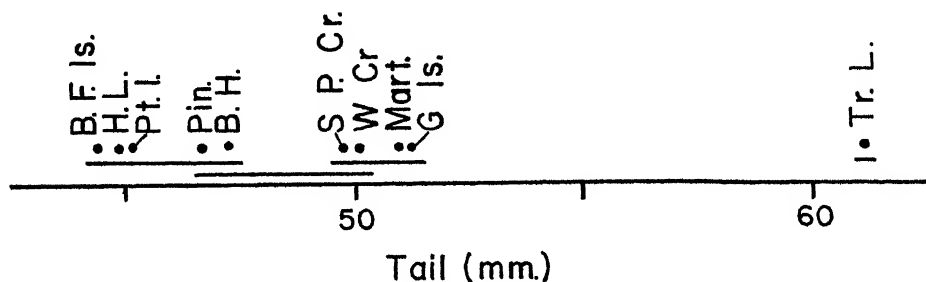


Fig. 5. Summary of contrasts of pairs of populations for tail length.
See legend, fig. 4.

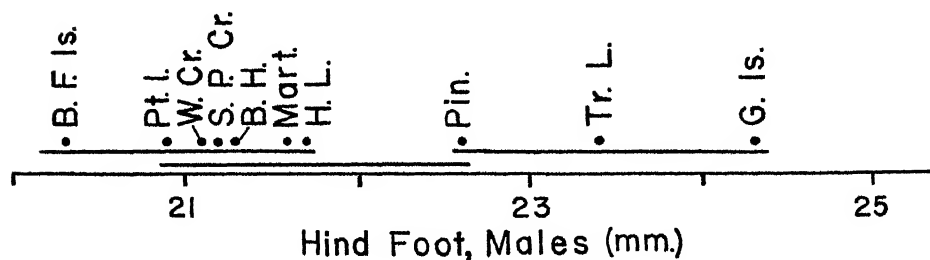


Fig. 6. Summary of contrasts of pairs of populations for hind-foot length of males.
See legend, fig. 4.

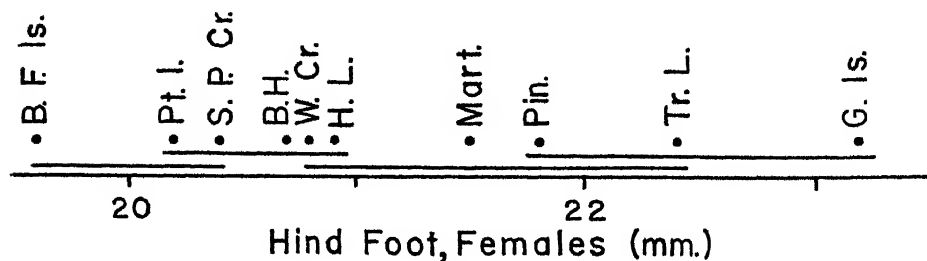


Fig. 7. Summary of contrasts of pairs of populations for hind-foot length of females.
See legend, fig. 4.

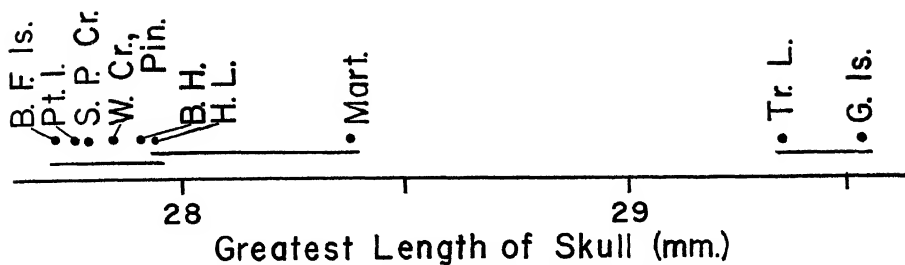


Fig. 8. Summary of contrasts of pairs of populations for greatest length of skull.
See legend, fig. 4; fig. 20.

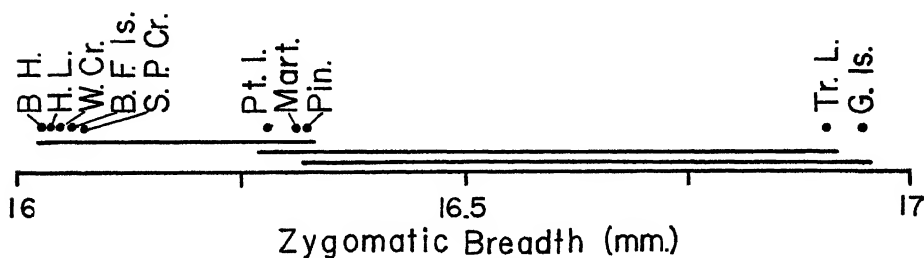


Fig. 9. Summary of contrasts of pairs of populations for zygomatic breadth.
See legend, fig. 4.

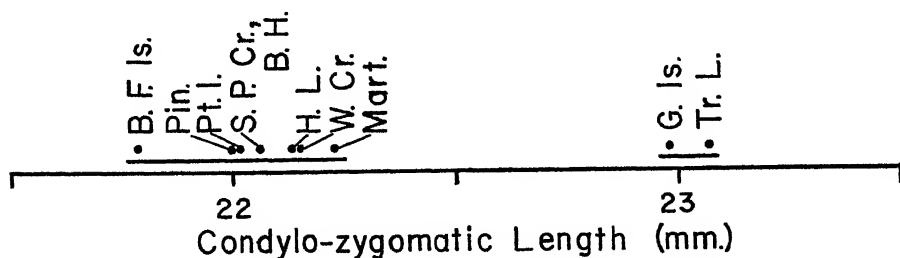


Fig. 10. Summary of contrasts of pairs of populations for condylozygomatic length.
See legend, fig. 4.

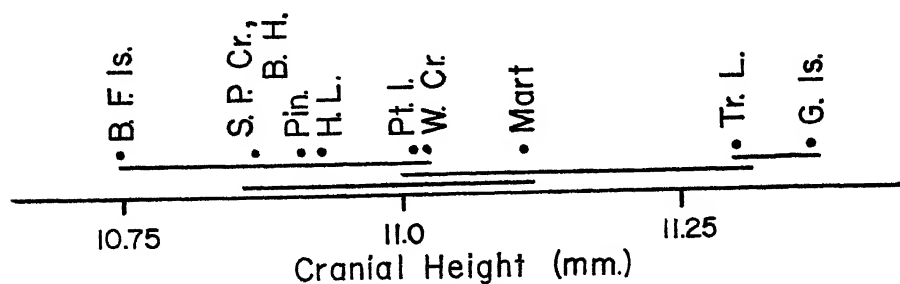


Fig. 11. Summary of contrasts of pairs of populations for cranial height.
See legend, fig. 4.

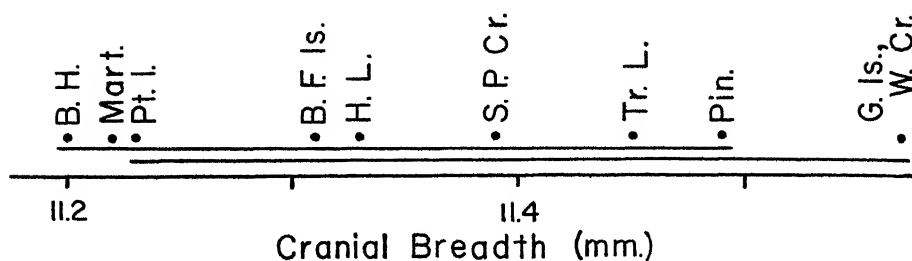


Fig. 12. Summary of contrasts of pairs of populations for cranial breadth.
See legend, fig. 4.

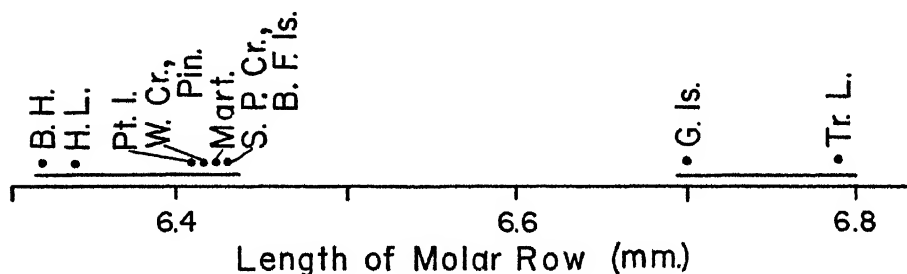


Fig. 13. Summary of contrasts of pairs of populations for length of molar row.
See legend, fig. 4.

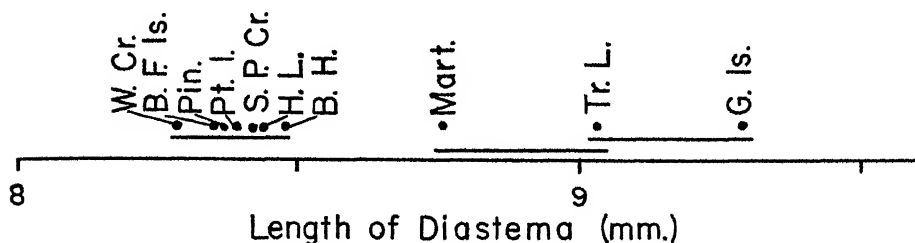


Fig. 14. Summary of contrasts of pairs of populations for length of diastema.
See legend, fig. 4.

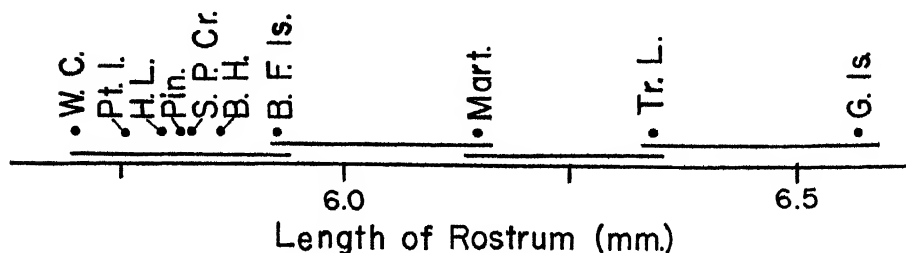


Fig. 15. Summary of contrasts of pairs of populations for length of rostrum.
See legend, fig. 4.

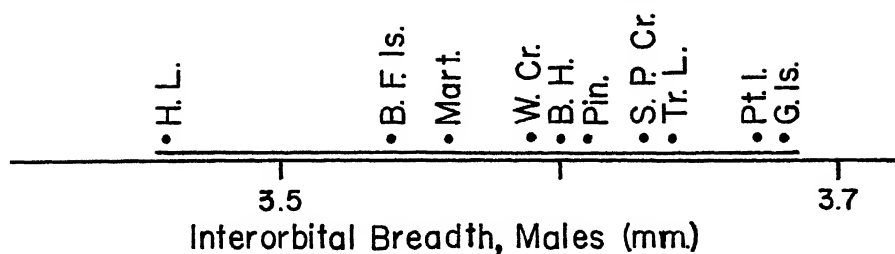


Fig. 16. Summary of contrasts of pairs of populations for interorbital breadth of males.
See legend, fig. 4.

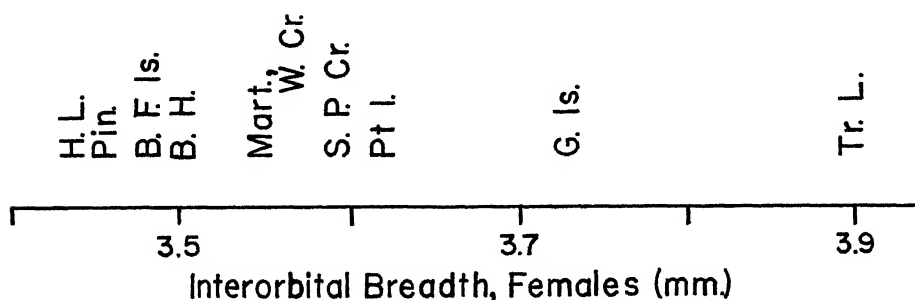


Fig. 17. Summary of contrasts of pairs of populations for interorbital breadth of females.
See legend, fig. 4.

In cranial height (fig. 11) the Grizzly Island and Tracy Lake group measured significantly larger than the Martinez population. The latter was not significantly larger than all smaller populations grouped together.

The Tracy Lake and Grizzly Island group had a significantly longer diastema than the Martinez population (fig. 14).

Additional contrasts between grouped populations were made for length of rostrum (fig. 15). The Grizzly Island and Tracy Lake group had a longer rostrum than the Martinez population, and the Martinez population was longer than all smaller populations when the latter were grouped together.

The interorbital breadth of females (fig. 17) from the Grizzly Island and Tracy Lake group was found to be greater than in all the numerically smaller populations grouped together.

MICROTUS CALIFORNICUS CALIFORNICUS

Upland populations.—Specimens from two localities previously described (B.H. and W. Cr.) represent populations of the race *Microtus c. californicus* from upland habitats. The two samples are similar in dimensions. Except for cranial breadth, no significant differences were found in the measurements of these two populations (figs. 4–17). Cranial breadth does not appear to have taxonomic significance, since the groupings of the populations suggested by this (fig. 12) are quite different from those suggested by other measurements, color, and nonmeasured skull characters. The measurement of cranial breadth has therefore been omitted from further consideration.

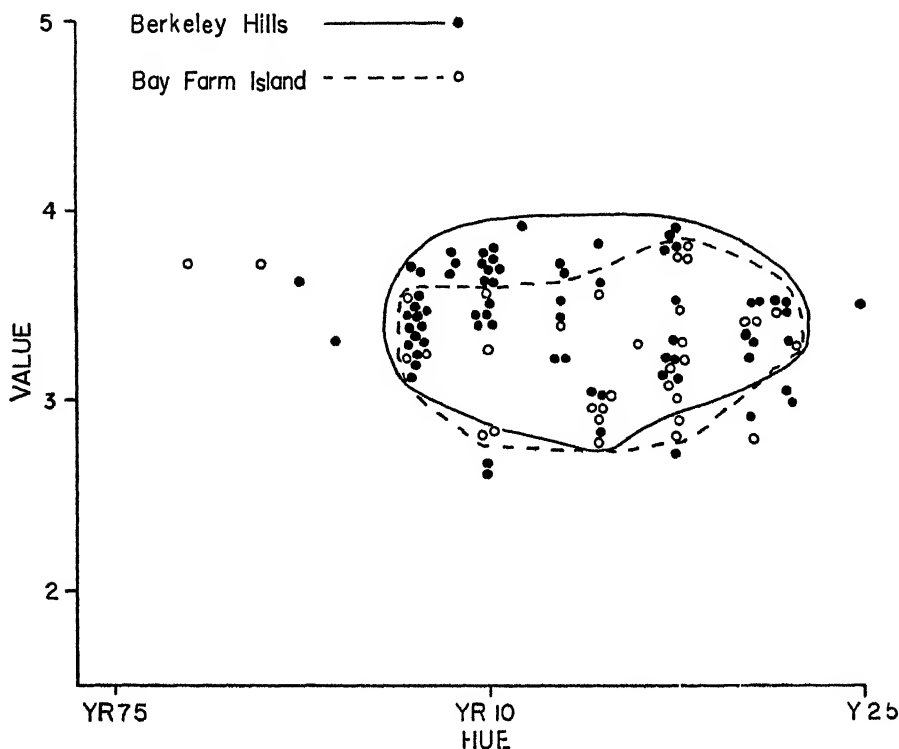


Fig. 18. Comparison of dorsal pelage color of specimens, class 6 and older, November April, of *M. c. californicus* (Berkeley Hills) and *M. c. "paludicola"* (Bay Farm Island). Enclosed areas include approximately 90 per cent of individuals in each sample.

Status of the Pinole population.—This population inhabits part of a very limited salt marsh on the southeast shore of San Pablo Bay. In general it is similar to populations of *Microtus californicus californicus* from upland localities. However, one measurement, that of hind foot, is significantly longer than that of the upland populations (figs. 6 and 7). Since there are relatively few specimens in the sample, and these were collected by several different persons, the difference may represent only a sampling or measuring error. It appears that this population should be considered as merely an undifferentiated representative of *M. c. californicus*.

Status of Microtus californicus paludicola.—In his description of this race Hatfield (1935) distinguished it from *M. c. californicus* on the basis of the following features: total length less, dorsal coloration darker, dorsal hairs darker basally, rostrum longer, brain case more narrow and more shallow. He also mentioned that the brain case is rounded anteriorly and that a flattening of the interorbital region and of the occiput is characteristic. Hooper (1944) mentioned a more reddish dorsum, longer nasals (relative to the molar row), and a posterior internal loop of M^2 as characters distinguishing *M. c. paludicola* from *M. c. californicus*.

In this study, samples from three populations which have been assigned to *M. c. paludicola* were analyzed: Point Isabel, Bay Farm Island (type locality),

and Hayward Landing. It was found that only the tail measurement separated these three populations from those of *M. c. californicus* (fig. 5). The tail length of *M. c. paludicola* was found to be significantly shorter. Also, the total length in the Point Isabel population was significantly shorter than in the *M. c. californicus* population (fig. 4), and the hind-foot length of females from Bay Farm Island was significantly less than that of *M. c. californicus* females (fig. 7). But in no other measurement did any of the three populations of *M. c. paludicola* differ significantly from *M. c. californicus*.

The color of *M. c. paludicola* was stated to be darker and redder than that of *M. c. californicus*. Figure 18 shows the almost complete overlap between the two groups in this regard. Several characters of the skull also are mentioned as separating *M. c. paludicola* from the upland race. Each of these was found to be inconsistent. For instance, only 8 of 19 skulls (classes 10-12) of the salt-marsh group showed the flattening of the interorbital region, while 12 of 36 from the upland areas showed the same characteristic.

This analysis has led me to conclude that, although the tail of populations assigned to *M. c. paludicola* and the hind foot of females from the type locality are shorter than in populations of *M. c. californicus*, these characters do not provide sufficient grounds for recognizing *M. c. paludicola* as a subspecies. Therefore, *M. c. paludicola* should be placed in the synonymy of *M. c. californicus*.

SAN PABLO CREEK POPULATION

Hooper (1944) characterized this population as intermediate between *M. c. aestuarinus* and *M. c. paludicola*. However, critical examination of a much larger sample than was available to him has led me to regard it as a separate subspecies. This race inhabits a very restricted area, and it can readily be distinguished from other races of *M. californicus*. The inclusion of this population within the subspecies *M. c. californicus* would result in a complex whose variation would appear to be greater than that found in the other races of the species. Furthermore, the differences between this form and its closest relative, *M. c. californicus*, are as great as those between several other currently recognized races of this species.

Microtus californicus sanpabloensis, new subspecies

Type.—Female, skin and skull; MVZ 123743, San Pablo Creek (salt marsh), Contra Costa County, California, December 23, 1958; collected by C. S. Thaeler, Jr.; original no. 748.

Range.—So far as known, limited to the salt marshes adjacent to the southeastern part of San Pablo Bay, northwest of Richmond and west of San Pablo and Giant, Contra Costa County, California.

Diagnosis.—Color: a dark subspecies with a yellowish cast; general color of the dorsum very dark, approaching black in extremes. Skull: posterior portion of the palatine deeply excavated, and with prominent transverse ridges ventral to these excavations. This subspecies has a narrow rostrum and inflated bullae.

Comparisons.—In no measurement does this subspecies differ significantly from *M. c. californicus* from the Berkeley Hills (see figs. 4-17). However, *M. c. californicus* differs in color, being lighter and more reddish (fig. 19). The skull of *M. c. californicus* is similar, but differs in that the posterior portion of the palatine is gently sloping, the rostrum tends to be broader, and the bullae tend to be less inflated. It differs from *M. c. aestuarinus* in being smaller and less reddish, from *M. c. eximus* from Marin County in being smaller, less reddish, and darker.

Measurements.—See tables 1-3.

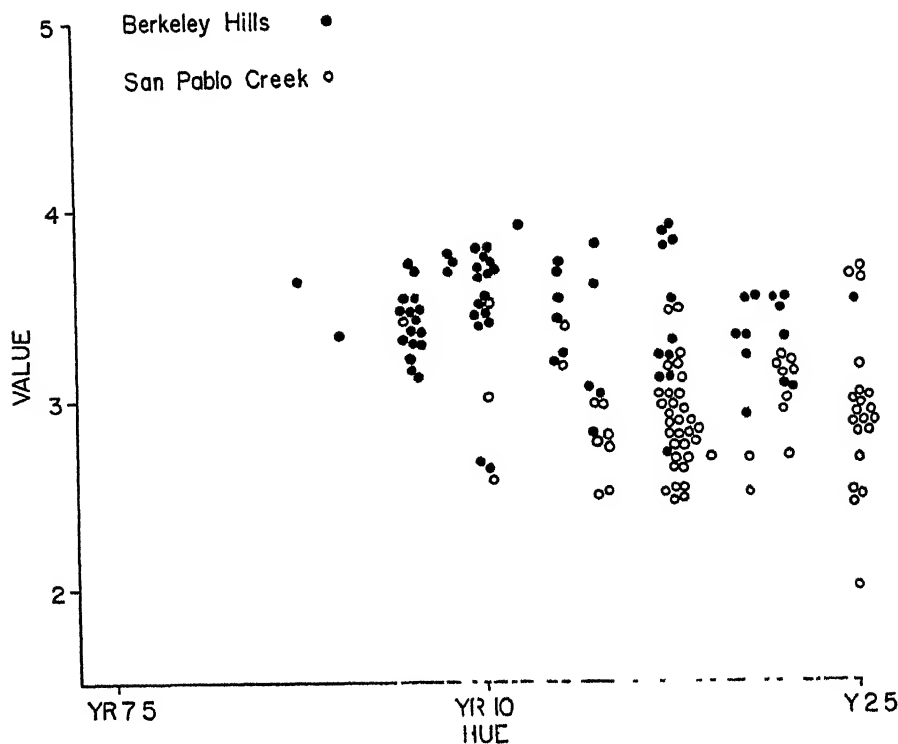


Fig. 19. Comparison of dorsal pelage color of specimens, class 6 and older, November-April, of *M. c. sanpabloensis* (San Pablo Creek) and *M. c. californicus* (Berkeley Hills).

Specimens examined.—Total of 84, all from Contra Costa County, California: Giant (salt marsh), MVZ 83519–83521, 122075–122076, 122085; $\frac{1}{2}$ mile S Giant (salt marsh), MVZ 83518; 2 miles W, $2\frac{1}{2}$ miles N Richmond, MVZ 70465; San Pablo Creek (salt marsh), MVZ 123685–123691, 123726–123739; 1 mile E mouth of San Pablo Creek, MVZ 83513–83517.

Remarks.—The range of *M. c. sanpabloensis* approaches that of *M. c. californicus* most closely just north of Giant. The few specimens at hand from Giant reflect this proximity, since they appear lighter, on the average, than specimens from San Pablo Creek.

MICROTUS CALIFORNICUS AESTUARINUS

Samples from two localities were referable to this subspecies. These were from Grizzly Island (type locality) and from Tracy Lake. This race is easily distinguished from *M. c. californicus* by its larger size, darker and more reddish coloration, and several relatively consistent characters of the skull, for example, the shape of the zygomatic arches and brain case, the procumbency of the incisors, and the shape of the lip of the auditory meatus. The two samples are very similar, and are distinct from all other samples. In only one measurement was there a significant difference between the two samples (fig. 6). The tail length of the Tracy Lake series (61.0 mm.) is appreciably longer than that of the Grizzly Island sample (51.3 mm.), which is not significantly longer than samples from several other localities. However, since the samples were obtained and measured

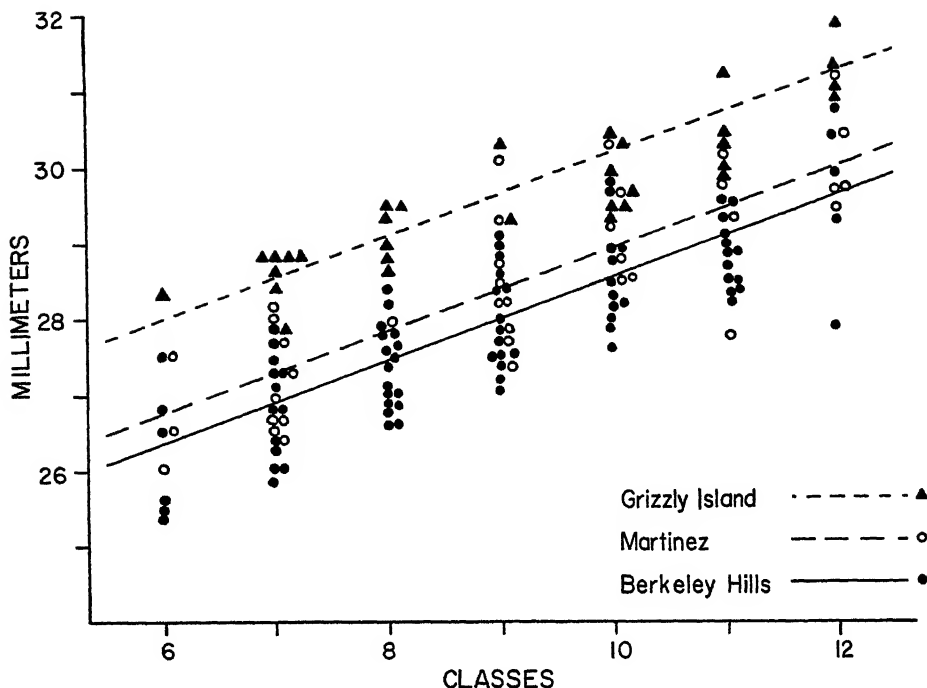


Fig. 20. Plot of greatest length of skull against class for three populations: *M. c. aestuarinus* (Grizzly Island), *M. c. californicus* × *aestuarinus* (Martinez), and *M. c. californicus* (Berkeley Hills).

by different collectors, this difference may be the result of different measuring techniques.

The color of the dorsal pelage of these samples is similar, although the Tracy Lake series is slightly lighter. Compared with the other samples, those of *M. c. aestuarinus* are distinctly redder and are equaled in darkness or amount of black pigment in the pelage only by the sample from Martinez.

In his description of the race *M. c. aestuarinus*, Kellogg (1918) mentions twenty or more features of the skull and teeth that tend to distinguish this race from *M. c. californicus*. However, the two subspecies overlap for most of these, and only specimens that show the extreme expression of the character can be correctly identified. Two characters, the shape of the zygomatic arch and the shape of the brain case, were found to be consistent in older animals. More precisely, 17 of 19 specimens in class 10 or above from the two series of this subspecies could be distinguished on the basis of shape of the zygomatic arches, while 26 of 28 specimens of *M. c. californicus* from Walnut Creek and the Berkeley Hills (class 10 or older) could be distinguished from *M. c. aestuarinus* by this character. On the basis of the shape of the brain case, all 14 specimens of *M. c. aestuarinus* (classes 11 and 12) could be distinguished from all 16 specimens of *M. c. californicus* of comparable age classes.

Two other consistently different characters were noted. The incisors of *M. c. aestuarinus* are more procumbent than those of *M. c. californicus*. In class 10 or

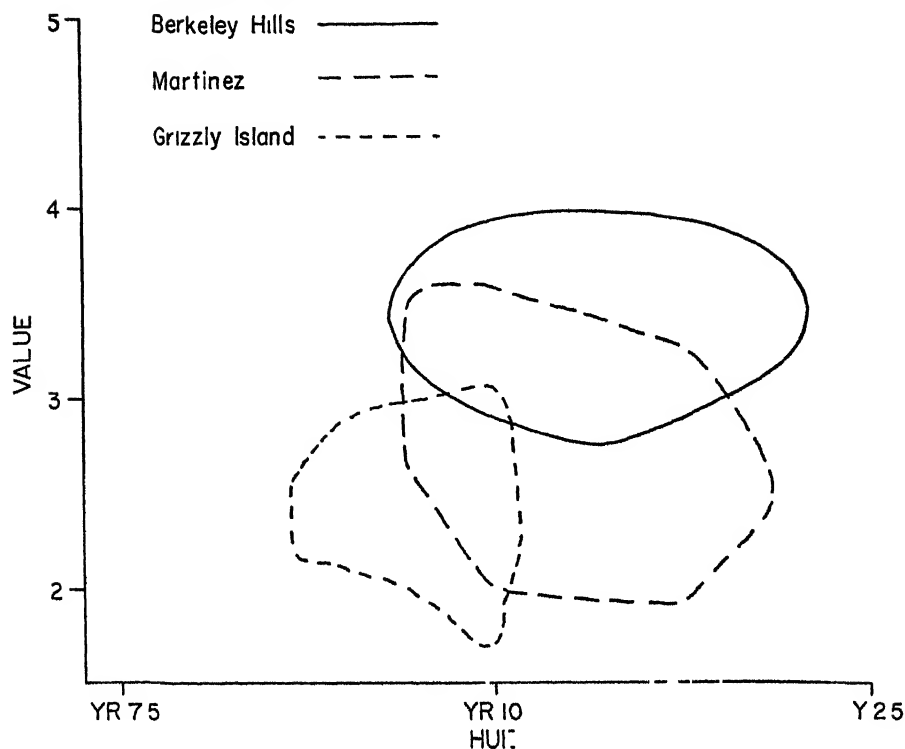


Fig. 21. Comparison of dorsal pelage color of specimens, class 6 and older, November April, of three populations: *M. c. aestuarinus* (Grizzly Island), *M. c. californicus* *aestuarinus* (Martinez), and *M. c. californicus* (Berkeley Hills). Enclosed areas include approximately 90 per cent of individuals in each sample.

older, 27 of 28 specimens of *M. c. californicus* and 18 of 19 specimens of *M. c. aestuarinus* could be properly recognized. A second character involves the thickness and amount of flare of the lip of the auditory meatus. This lip was thinner and more flared in *M. c. californicus*. On the basis of this character, 27 of 28 specimens of *M. c. californicus* and all 19 specimens of *M. c. aestuarinus* (classes 10–12) could be properly identified.

THE MARTINEZ POPULATION

Although Hooper (1944) referred this population to *M. c. aestuarinus*, a more critical examination based on more material than was available to him has led me to a different conclusion. Admittedly, the Martinez population resembles *M. c. aestuarinus* in the amount of black in the dorsal pelage; however, it averages more yellow or less red than *M. c. aestuarinus*. Furthermore, an analysis of the measurements of the body and skull indicate that, in general, the Martinez population is smaller than *M. c. aestuarinus* in total length, hind foot, greatest length of skull, zygomatic breadth, condylozygomatic length, cranial height, length of molar row, length of diastema, and length of rostrum.

Nor does the Martinez population closely resemble *M. c. californicus*, since the

former is darker and longer in total length, length of hind foot (females), greatest length of skull, length of diastema, and length of rostrum. It differs from *M. c. sanpabloensis* in that it is longer in the above-mentioned characters and more reddish.

If the attempt is made to relate the Martinez population to either *M. c. aestuarinus* or *M. c. californicus* on the basis of nonmeasurable skull characters, no conclusive results can be obtained. Identification by the use of these characters, when applied to 16 specimens of the older age classes (10–12) from the Martinez population, gave the following results: 12 were referable to *M. c. californicus* and 3 to *M. c. aestuarinus* by the shape of the zygomatic arches (one with broken zygomatic arches); on the basis of the degree of procumbency of the incisors, 9 were referable to *M. c. californicus* and 7 to *M. c. aestuarinus*; on the basis of the lip of the auditory meatus, 8 were referable to *M. c. californicus* and 8 to *M. c. aestuarinus*; on the basis of the brain-case shape (classes 11 and 12 only), 6 were referable to *M. c. californicus* and 3 to *M. c. aestuarinus*. Although each of these characters correctly identified at least 90 per cent of all specimens of either *M. c. californicus* or *M. c. aestuarinus*, with regard to the Martinez populations these characters would serve to identify the available specimens only 50–80 per cent of the time if this population were referred to *M. c. californicus*, or 20–50 per cent of the time if it were referred to *M. c. aestuarinus*.

Therefore it can be concluded that the Martinez population cannot properly be referred to any existing race. I have concluded that it should be designated *M. c. californicus* \times *aestuarinus*. This view is discussed below.

DISTRIBUTION OF MICROTUS IN COMPARISON TO SOME OTHER INHABITANTS OF SALT MARSHES

Although no other higher vertebrate is now known that shows the same pattern of distribution as that of *Microtus californicus* in the salt marshes of San Francisco Bay, several show parallels with it. Within the area are two species of harvest mice: *Reithrodontomys megalotis* is an upland species; *R. raviventris* is restricted to the salt marshes. The subspecies *R. raviventris raviventris* ranges around the southern arm of the Bay, north to the marsh at San Pablo Creek, and apparently is absent from the marsh at Pinole. A second subspecies, *R. r. halicoetes*, occurs in the Martinez marshes, in the Sacramento–San Joaquin delta, and on Grizzly Island. Here, then, the discontinuity of marshes between San Pablo Creek and Martinez forms a break between the two subspecies of *R. raviventris* just as it does between *M. c. sanpabloensis* and the unrelated Martinez population (*M. c. californicus* \times *aestuarinus*). Only the upland form is represented in the isolated marsh at Pinole.

Various forms of the genus *Sorex* have distributions paralleling those of *Microtus* in this area. *Sorex sinuosus* is found in the marshes north of Suisun Bay but not at Martinez, just as *M. c. aestuarinus* is found in the marshes north but not south of Suisun Bay. *Sorex vagrans halicoetes*, a form restricted to salt marshes, is found from San Pablo Creek marshes south around the southern end of the bay. Here again the discontinuity of salt marshes between San Pablo Creek and Martinez results in a barrier to salt-marsh forms.

The pattern of distribution of the races of the song sparrow, *Melospiza melodia*, shows similarity to that of this vole. Within this area *M. melodia* is represented by four races; one is an upland form and the other three are limited to various salt marshes. One marsh race, *M. m. pusillula*, is limited to the southern end of the bay, north to Stege, Contra Costa County (just north of Point Isabel). *Melospiza melodia samuelis* is limited to the marshes around San Pablo Bay; Marshall (1948) reports it from both San Pablo Creek marsh and Pinole. *Melospiza melodia marilaris* is limited to marshes around Suisun Bay.

DISCUSSION

The tendency for both birds and mammals to evolve differentiated forms in these salt marshes has been noted. The data at hand are sufficient to permit speculation about some of the factors involved in the differentiation of *Microtus californicus* and the relationships of the populations studied. The lack of differentiation between the upland population and that found at Pinole is not surprising. The marshes here are isolated from other marshes and are limited in extent. They appear closely connected with the adjacent upland population by the areas of suitable habitat that occur along the stream that empties into the bay here. The small size of the marsh population and the relative lack of isolation suggest that any tendency toward differentiation in the marsh, as it now exists, has been limited by a constant swamping out of the marsh population by that from the adjacent upland. This lack of differentiation is in accord with the habitat preference suggested by trapping results. The eleven specimens that I secured from this area were all taken along the edges of dikes and along the railroad embankment. No mice were caught on lower ground in the marsh proper, although traps were set there. Most signs of *Microtus* activity were likewise limited to the dikes and the railroad embankment. Furthermore, neither of the other typical salt-marsh mammals, *Reithrodontomys r. raviventris* and *Sorex vagrans halicoetes*, both found in nearby San Pablo Creek marsh, are known from this marsh. Only *Reithrodontomys megalotis* and *Sorex ornatus*, both typical of the adjacent upland, have been taken from this locality. (Specimens of these species from the Pinole salt marsh are in the MVZ collection.)

Farther south the situation is somewhat more complicated. The moderately extensive marshes at San Pablo Creek support a differentiated population of voles (*M. c. sanpabloensis*). This population resembles *M. c. californicus* in all respects except color and the three skull characters mentioned. It is geographically isolated from the Martinez population and can be distinguished from it by its smaller measurements. Also, it does not show the mixing of the skull characters of *M. c. aestuarinus* and *M. c. californicus* found at Martinez. Therefore, it appears to be a population derived from *M. c. californicus* by differentiation *in situ*, in this salt-marsh environment. However, south of here, in the very extensive marshes around the southern arm of the bay, the vole populations remain undifferentiated from the adjacent populations of *M. c. californicus*. That the voles in these two areas of salt marsh differ is perhaps to be expected, in view of the fact that the marshes at San Pablo Creek are not connected with those farther south. Furthermore, the song sparrows differ racially in the two areas. *Melospiza melodia pusillula* in-

habits the marshes around the southern arm of the bay, while *M. m. samuelis* inhabits the marsh at San Pablo Creek. Although two other forms, *Sorex vagrans halicoetes* and *Reithrodontomys r. raviventris*, inhabit both localities, the situation is not comparable, since these represent different species from those found in the adjacent uplands.

The unexpected result, then, is that the vole populations in the marshes around the southern arm of the bay remain essentially undifferentiated from the upland form, whereas the voles from the San Pablo Creek marsh have evolved into a distinct subspecies. This development has not been caused by a difference in the amount of isolation afforded the two marsh populations, since they appear to be equally well isolated from (or connected to) adjacent upland populations. Voles are found throughout the hills which surround the bay, especially in moist areas. However, much of the gently sloping area between the hills and the bayside marshes was probably too dry to support vole populations regularly. This supposition is difficult to test, for much of the area has been altered by urban development and irrigated farming. However, riparian habitats along stream banks did provide avenues of connection between upland localities and both of these salt marshes.

Nor is there any evidence to support the argument that the southern population has failed to differentiate because it has been in existence a shorter time. Marshall (1948) considers that the San Pablo Creek marsh is a "young" marsh, while at least some marshes around the southern end of the bay are "old" marshes. He mentions the marsh at the mouth of Alviso Slough as an example of an "old" marsh.

Size of population is another factor that may be important in these considerations. The marshes at San Pablo Creek are much smaller than those around the southern arm of the bay. Therefore it can be assumed that the size of their vole populations also is quite different. A. H. Miller (1956) and others have stressed the importance of small populations in increasing the speed of diversification. Thus the much larger population of voles in the southern marshes may not have developed racially, while the smaller San Pablo Creek population has.

However, the most likely explanation seems to be that the environment of the marshes around the southern arm of the bay does not provide conditions that would result in the differentiation of either the morphological or the pelage color characters studied here. The most significant differential character of *M. c. sanpabloensis* is its dark color, but conditions in the southern marshes do not appear to favor the development of darker pigmentation. Grinnell (1913), in his discussion of the fauna of the bay, points out that the various faunal components develop their darkest pigmentation in the marshes around Suisun Bay, the least saline. (The southern arm of San Francisco Bay is the most saline.)

Apart from *Microtus californicus*, this tendency is best demonstrated by the song sparrows. *Melospiza melodia samuelis* and *M. m. maxillaris* are both darker than *M. m. gouldii*. However, *M. m. pusillula* from the southern end of the bay, although differentiated from the upland populations of *M. m. gouldii* by its smaller size and yellow wash on the breast (Marshall, 1948), is not distinctly darker than the upland form.

A similar condition can be observed in *R. r. raviventris*. George Fisler, who is currently studying these harvest mice, has informed me that the mice from Melrose Marsh and marshes near Redwood City (San Mateo County) appear somewhat lighter dorsally than *R. r. raviventris* from San Pablo Creek marsh.

Although the marshes at Point Isabel are now not continuous with those at San Pablo Creek, they have been connected within the past seventy years. Destruction of the natural habitat has brought about this change. The sample from this locality, however, shows no similarity to *Microtus californicus sanpabloensis*. The marshes here have always been limited in extent, and recent filling has further decreased their size. Hence the population of voles here is probably very small. It seems likely that if *M. c. sanpabloensis* ever ranged this far south it existed in such small numbers that, once isolated, it has been swamped out by influxes of undifferentiated mice from adjacent areas.

The relationships of the Martinez population are quite evident. It is intermediate in size and color between *Microtus californicus californicus* and *M. c. aestuarinus*. Furthermore, the color appears to be more variable than in other populations. (This would explain the lack of apparent seasonal color variation, since the population variation seems to exceed the seasonal variation.) Several characters of the skull also show the intermediacy of this population.

There are three processes that might result in such an intermediate population. One would be the adaptation of the population to various intermediate situations along a cline from one ecological extreme to another. In this situation, however, no such cline of ecological conditions exists, nor is there any tendency for other populations which are intermediate in position to show such a trend. The Walnut Creek population, although geographically intermediate between the Berkeley Hills and the Martinez populations, is in no way morphologically intermediate.

The other possible processes are the development of a differentiated form from either of the possible parent forms (*M. c. californicus* or *M. c. aestuarinus*) under the isolation afforded by the marsh, or the development of a differentiated form by the secondary contact or intergradation of these two existing subspecies. On the basis of size and color the Martinez population lies between the other two races. From this it would appear that the Martinez population could have been derived from either. However, the mixing of skull types and the greater color variation can be explained only in terms of secondary contact.

The marshes east of Martinez are relatively well isolated from other vole habitats. The unfavorable habitat to the east isolates this marsh from the areas inhabited by *M. c. aestuarinus*. However, the periodic occurrence of high tides in the bay and spring floods in the river systems provide for frequent flooding of areas within the range of *M. c. aestuarinus*. Such floods probably serve to carry voles into the marshes at Martinez. Johnston (1957) mentions seeing *Microtus* sitting on floating wood during periods of inundation of salt marshes.

The marshes east of Martinez are partially isolated from the habitats of *M. c. californicus* also. The low hills south of the marshes are dry much of the year and not heavily covered with grass. Although they may support low densities of *Microtus* at times, only the one or two permanent streams draining into the marsh form small but continuous connections between the habitats of the two races.

These conditions of partial isolation would allow small numbers of the parental forms to enter the Martinez marsh and by interbreeding establish a population, the present form of which would then be the result of selection upon the genetic makeup of both parental types. Small but continual influxes of the parental types would tend to maintain the greater variation observed in this population.

Although the Martinez population is sufficiently distinct to be separable from existing subspecies and thus to warrant recognition as a distinct subspecies, I prefer at this time to designate it merely as *M. c. californicus* \times *aestuarinus*. Since, as has been shown, it cannot properly be assigned to any extant race, this more conservative course takes cognizance of the dichotomy of its origin and implies its intermediacy in characters.

This course is followed because the scope of the present work is too narrow to yield an understanding of the pattern of variation within this species. Should small, relatively isolated populations resulting from the secondary contact of two well-marked subspecies be found to occur frequently throughout the range of *M. californicus*, the application of a trinomial to this population would not be warranted. However, if further studies of the species demonstrate that such situations are uncommon, I believe that the use of the trinomial would be justified.

It might be argued that, since the San Francisco Bay area has provided an unusual situation with regard to subspeciation of palustrine vertebrates, the Martinez population is, *ipso facto*, unusual. However, such a conclusion must await the result of an intensive study of the whole species.

SUMMARY

Ten samples of *Microtus californicus* from salt marshes in Alameda and Contra Costa counties and from several adjacent upland and marsh areas were studied. An analysis of intrapopulational variations showed that most of the measurements taken varied significantly with age. In most of these measurements no significant differences between males and females were found, but it is suggested that this similarity is probably an anomaly of the age index used. The color of the dorsal pelage showed no sex or age difference, but a seasonal variation was found.

Comparisons of these samples showed that one salt-marsh population is sufficiently distinct to warrant recognition as a new subspecies. *Microtus californicus sanpabloensis* is described from the marshes at the mouth of San Pablo Creek, Contra Costa County; a second salt-marsh population, formerly recognized as *M. c. paludicola*, was found to be indistinguishable from *M. c. californicus*. A third population from salt marshes east of Martinez is regarded as intermediate between two extant subspecies and consequently is referred to as *M. c. californicus* \times *aestuarinus*.

The distributions of salt-marsh forms of harvest mice, shrews, and song sparrows are compared to those of this vole.

Variation in *Microtus californicus* is discussed with reference to the distribution and extent of the salt marshes. *Microtus c. sanpabloensis* is considered to have been derived from *M. c. californicus*. Evidence is given to support the conclusion that the Martinez population, although distinct, has been derived from the secondary contact of *M. c. californicus* and *M. c. aestuarinus*.

TABLE 1

(N=number of specimens. $\hat{Y}_{9.0}$ =estimate of mean at age class 9. S_y/\bar{z} =standard deviation at given age (\bar{z}).)

Population	Total length	Tail length	Greatest length of skull	Zygomatic breadth	Condylzygomatic length
<i>M. c. aestuarinus</i>					
Tracy Lake.....N	20	20	17	16	18
$\hat{Y}_{9.0}$	187.8	61.1	29.35	16.81	23.06
S_y/\bar{z}	10.10	3.42	.200	.519	.606
Grizzly Island.....N	32	32	32	24	32
$\hat{Y}_{9.0}$	181.3	51.3	29.53	16.90	22.98
S_y/\bar{z}	7.72	5.12	.077	.515	.416
<i>M. c. californicus</i> × <i>aestuarinus</i>					
Martinez.....N	38	39	37	36	37
$\hat{Y}_{9.0}$	175.1	51.0	28.37	16.37	22.23
S_y/\bar{z}	7.28	3.85	.121	.473	.576
<i>M. c. californicus</i>					
Walnut Creek.....N	28	28	27	27	27
$\hat{Y}_{9.0}$	171.3	50.1	27.85	16.10	22.15
S_y/\bar{z}	6.04	3.67	.065	.335	.297
Berkeley Hills.....N	77	78	81	79	81
$\hat{Y}_{9.0}$	166.7	47.6	27.91	16.06	22.06
S_y/\bar{z}	7.46	3.97	.073	.471	.523
Pinole.....N	11	11	11	11	11
$\hat{Y}_{9.0}$	168.4	46.8	27.85	16.38	22.00
S_y/\bar{z}	7.66	3.91	.159	.381	.450
<i>M. c. "paludicola"</i>					
Point Isabel.....N	23	24	23	23	23
$\hat{Y}_{9.0}$	157.3	45.2	27.76	16.31	22.01
S_y/\bar{z}	8.13	3.88	.080	.335	.271
Bay Farm Island.....N	26	26	28	28	28
$\hat{Y}_{9.0}$	165.8	44.5	27.72	16.12	21.79
S_y/\bar{z}	8.11	4.42	.058	.291	.258
Hayward Landing.....N	13	13	19	20	19
$\hat{Y}_{9.0}$	168.0	45.0	27.94	16.08	22.13
S_y/\bar{z}	7.21	3.46	.157	.504	.573
<i>M. c. sanpabloensis</i>					
San Pablo Creek.....N	79	79	80	78	80
$\hat{Y}_{9.0}$	169.6	49.9	27.80	16.15	22.06
S_y/\bar{z}	8.02	4.20	.057	.376	.459

TABLE 2

(N=number of specimens. $\hat{Y}_{9.0}$ =estimate of mean at age class 9. S_y/\bar{x} =standard deviation at given age (\bar{x}).)

Population	Cranial height	Cranial breadth	Length of molar row	Length of diastema	Length of rostrum
<i>M. c. aestuarinus</i>					
Tracy Lake.....N	18	16	20	19	17
$\hat{Y}_{9.0}$	11.30	11.45	6.79	9.03	6.34
S_y/\bar{x}	.197	.325	.264	.273	.340
Grizzly Island.....N	32	28	32	32	32
$\hat{Y}_{9.0}$	11.37	11.57	6.70	9.29	6.57
S_y/\bar{x}	.309	.341	.236	.258	.311
<i>M. c. californicus</i> \times <i>aestuarinus</i>					
Martinez.....N	37	39	39	38	36
$\hat{Y}_{9.0}$	11.06	11.22	6.42	8.76	6.15
S_y/\bar{x}	.376	.385	.266	.364	.318
<i>M. c. californicus</i>					
Walnut Creek.....N	26	24	28	28	27
$\hat{Y}_{9.0}$	11.02	11.57	6.42	8.29	5.70
S_y/\bar{x}	.218	.389	.290	.222	.211
Berkeley Hills.....N	81	81	81	81	81
$\hat{Y}_{9.0}$	10.87	11.20	6.32	8.48	5.87
S_y/\bar{x}	.253	.325	.239	.304	.275
Pinole.....N	11	11	11	11	11
$\hat{Y}_{9.0}$	10.91	11.49	6.42	8.37	5.82
S_y/\bar{x}	.295	.272	.158	.225	.219
<i>M. c. "paludicola"</i>					
Point Isabel.....N	23	24	24	24	23
$\hat{Y}_{9.0}$	11.01	11.23	6.41	8.39	5.76
S_y/\bar{x}	.273	.332	.169	.280	.281
Bay Farm Island.....N	28	27	30	30	28
$\hat{Y}_{9.0}$	10.75	11.31	6.43	8.36	5.93
S_y/\bar{x}	.328	.330	.205	.228	.268
Hayward Landing.....N	19	19	20	20	19
$\hat{Y}_{9.0}$	10.93	11.33	6.34	8.44	5.80
S_y/\bar{x}	.288	.287	.204	.332	.261
<i>M. c. sanpabloensis</i>					
San Pablo Creek.....N	81	80	83	82	80
$\hat{Y}_{9.0}$	10.87	11.39	6.43	8.42	5.83
S_y/\bar{x}	.211	.262	.226	.261	.248

TABLE 3
(N=number of specimens. Y=mean. S=standard deviation.)

Population	Hind-foot length		Interorbital breadth	
	Males	Females	Males	Females
<i>M. c. aestuarinus</i>				
Tracy Lake.....N	15	5	12	3
Y	23.4	22.4	3.64	3.90
S	1.06	.894	.150	.100
Grizzly Island...N	11	21	11	21
Y	24.3	23.2	3.68	3.73
S	1.22	.733	.160	.158
<i>M. c. californicus</i> × <i>aestuarinus</i>				
Martinez.....N	13	25	13	24
Y	21.6	21.5	3.56	3.55
S	.875	.644	.126	.128
<i>M. c. californicus</i>				
Walnut Creek.....N	19	9	19	8
Y	21.1	20.8	3.59	3.55
S	.931	.833	.123	.109
Berkeley Hills.....N	33	41	34	41
Y	21.3	20.7	3.60	3.51
S	1.20	.895	.135	.159
Pinole.....N	7	4	7	4
Y	22.6	21.8	3.61	3.45
S	.978	.957	.149	.173
<i>M. c. "paludicola"</i>				
Point Isabel.....N	10	13	10	13
Y	20.9	20.2	3.67	3.62
S	.738	1.28	.212	.121
Bay Farm Island.....N	16	12	16	13
Y	20.3	19.6	3.54	3.48
S	1.19	.483	.115	.169
Hayward Landing.....N	6	7	12	8
Y	21.7	20.9	3.46	3.44
S	1.48	.689	.343	.151
<i>M. c. sanpabloensis</i>				
San Pablo Creek.....N	43	39	41	39
Y	21.2	20.4	3.63	3.59
S	1.21	.641	.178	.130

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ECOLOGY AND SOCIAL BEHAVIOR OF THE COATI, NASUA NARICA ON BARRO COLORADO ISLAND PANAMA

BY
JOHN H KAUFMANN



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ECOLOGY AND SOCIAL BEHAVIOR OF THE COATI, *NASUA NARICA*, ON BARRO COLORADO ISLAND, PANAMA

BY
JOHN H. KAUFMANN

(A contribution from the Museum of Vertebrate Zoölogy
of the University of California)

INTRODUCTION

THIS REPORT SUMMARIZES A STUDY of the ecological adaptations, especially behavioral, of the coati (*Nasua narica*) in its natural habitat. The Smithsonian Institution's field station on Barro Colorado Island, Canal Zone, was the site of the study. Although conditions on Barro Colorado cannot be considered primeval, they are less affected by man than those in other parts of Latin America where coatis are found. Observations on both wild, free-living animals and on captives were made from July 1, 1958, to June 29, 1960.

The coatis are the most social and most diurnal members of the American Procyonidae. Known by a wide variety of common names from Arizona to Argentina, the several species are conspicuous members of the fauna throughout their range. "Coati" is derived from the Tupian "cua" (belt) plus "tim" (nose), and probably refers to the animal's habit of sleeping with the nose against the belly. "Coati-mondi" refers specifically to solitary coatis—adult males are solitary; females and young live in bands—but the name is generally misused in English to refer to all coatis. The confusion over the status of solitary and social coatis led originally to the use of separate scientific names (*Nasua solitaria* Schinz and *Nasua sociabilis* Schinz) for old males and for band members described from Brazil (Allen, 1916). The confusion persists in the welter of common names, as in the use of "gato solo" (lone cat) for referring to all coatis in much of Panama.

COATI LITERATURE

Until now there has been no careful study of the coati, and the English literature consists almost entirely of popular and semipopular accounts based more on hearsay and speculation than on observed facts. Even the best of these (e.g., Chapman, 1929) present a few apparently accurate but fragmentary observations plus an abundance of speculation. Since the facts cannot readily be separated from fancy unless one is very familiar with coatis, such accounts are of limited value. More careful accounts based on closer personal contact with the animals over a long period of time are available in the Latin American literature (Alvarez del Toro, 1952; Cabrera and Yepes, 1940; Gaumer, 1917; Azara, 1838). In addition to his own observations, Leopold (1959) made wise use of Spanish language sources in producing one of the most reliable accounts of coati biology in the English language. However, the best of the accounts available are only a few pages long, and they present limited information on the general life history of the coati.

The information presented in this paper applies strictly to the coatis I observed on Barro Colorado, and generalizations about coatis elsewhere should be made with extreme caution. Specific details of social organization, activity patterns, food habits, and interspecific relations may vary widely in different areas.

MORPHOLOGY AND TAXONOMY

A slender tail as long as the body, often carried erect, and a mobile snout that extends well beyond the end of the lower jaw are the coati's most conspicuous features (pl. 1). The standard measurements of adult males of *Nasua narica* from several collections made throughout Central America range as follows: total length, 1,067–1,265 mm; tail, 475–635 mm; hind foot, 98–118 mm; ear, 38–44 mm. The few reliable weights that are available indicate a range from about 4 to 6 kilograms or more. A typical adult male from Barro Colorado weighed just 12 pounds (5.5 kg) and had a total length between 1,100 and 1,150 mm. Adult males especially tend to put on fat temporarily when food is abundant, and higher weights are probable.

Females are smaller than males, and the several collections showed the following range of standard measurements: total length, 980–1,194 mm; tail, 470–598 mm; hind foot, 83–116 mm; ear, 25–44 mm. A typical adult female on Barro Colorado had a total length of 1,046 mm, a tail length of 529 mm, and varied in weight from 8¾ pounds (4 kg) when sick and thin to 12 pounds (5.5 kg) after several weeks in captivity. Her normal weight was about 10 or 11 pounds (5 kg).

The genus *Nasua* includes several species in North, Central, and South America. *Nasua narica* ranges from southern Arizona south through Panama; and *Nasua nelsoni*, which might be considered a subspecies of *Nasua narica*, is found only on Cozumel Island, Quintana Roo, Mexico. The South American coatis are badly in need of a proper taxonomic revision, which would probably reduce many of the described species to subspecific status. Similarly the many described subspecies of *Nasua narica* can profitably be reduced to the three recorded by Hall and Kelson (1959).

Writing of the great variation in color and cranial characters on which the subspecies are based, Burt and Hooper (1941) state, "Most of the variation apparently is attributable to differences in age, sex, and individuals." They also found that "the general color becomes progressively darker on the average from north to south." Hershkovitz (1951), working with material classified in the subspecies *Nasua narica isthmica* Goldman, *richmondi* Goldman, *panamensis* Allen, and *bulata* Allen, noted:

Among coatis the great amount of polychromatism independent of sex obscures the geographic cline in color and has led to a multiplication in the number of named forms. . . . Further complicating the study of geographical variation in color are instances of partial or complete erythasm and melanism, not as fixed individual characters but as transitory pelage phases. Adequate series demonstrate the absolute unreliability of cranial characters for distinguishing any of the described forms from the others.

Allen (1906) also commented on the immense range of color in a single series, with the extremes connected by a full set of intermediates.

Coatis on Barro Colorado also show much color variation. Detailed observations

of over fifty individuals for periods of up to two years each, plus casual records of many more coatis, show conclusively that color differences may be independent of age and sex, and that the same individual may change color from molt to molt. The most common coat color on Barro Colorado is chocolate brown, with an abundance of light-tipped hairs forming the pale wash over the shoulders. The shoulders are yellowish, and the facial markings are whitish. None of the Barro Colorado coatis observed is as pale as those I have seen in Arizona, but there is a complete color gradation from almost black to pale sandy brown, and some individuals are bright reddish brown. Color changes in the same individual, as from slaty gray-brown to "normal" brown, were observed repeatedly. Two young males molted from bright reddish to chocolate brown except for their tails, which were still red when the animals were last seen several months later.

During the reproductive season both males and females tend to fade to a pale reddish, particularly on the shoulders and rump. Darling (1937) reported a similar paleness in the coat of lactating red deer. In coatis this seems to be due more to the loss of the darker hair tips, exposing the lighter underfur, than to replacement or fading of the dark hair. During this period the fur becomes quite sparse and mangy-looking; females with young can easily be recognized by the color and condition of their coats for several months after the young are born. Perhaps the added physiological demands of the breeding season are responsible for the degeneration of pelage. This degeneration was observed consistently in both wild breeding females and in captive breeding females receiving the same diet they had been eating all year, indicating that a seasonal change in diet was not responsible. Nonbreeding adult females, both captive and in the wild, failed to show a change in coat.

Attempts to trace the pattern of molts in coatis of various ages by bleaching the fur were unsuccessful, for each bleached patch faded gradually over a period of several months. However, occasional rapid molts, apparently completed in a few weeks, were observed at various seasons. Three solitary males, one of them recently having become adult, apparently underwent a complete molt between late June and mid-July, 1959. Gaumer (1917) stated that the pelts of coatis in Yucatan are at their best from September to January and that they tend to become duller and thinner during the first part of the year. This agrees with my observations on Barro Colorado. Whatever the pattern of molts—and this subject certainly deserves more careful study—individual animals are known to have changed color one or more times, and these changes could not be consistently correlated with season, sex, or age.

DESCRIPTION OF BARRO COLORADO ISLAND

Location and topography.—Until the construction of the Panama Canal, Barro Colorado was a hill along the lower Chagres River approximately in the center of the isthmus. When the river was dammed to form Gatun Lake, the rising waters isolated Barro Colorado as the lake's largest island. Rising 452 feet above the lake surface and 537 feet above sea level, the irregularly shaped island has an indented shoreline over 25 miles long (40 km), a maximum diameter of over 3 miles (5.5 km), and an area of 6 square miles (3,884 acres or 15.7 km²). The eastern half of

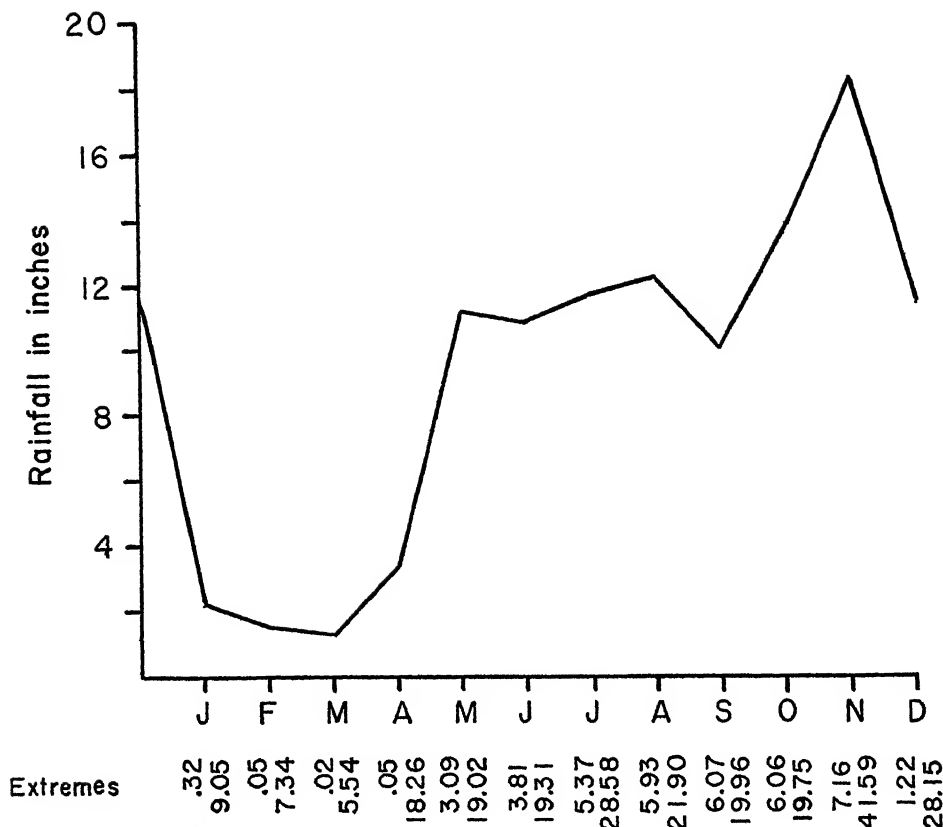


Fig. 1. Rainfall, Barro Colorado Island. Monthly averages and extremes, 1926-1960.

the island rises sharply from the lake, with a complex pattern of ridges and ravines up to 100 feet deep. From its highest point the island slopes back more gently and evenly to the western shore, which is separated from the mainland by a shallow channel 600 yards wide. The detailed geology of Barro Colorado was presented by Woodring (1958).

Climate.—Located at $9^{\circ}10'$ north latitude and $79^{\circ}51'$ west longitude, the island is a tropical rain forest locality with some monsoon forest characteristics. The climate was discussed at length by Allee (1926a) and Kenoyer (1929). Since then more information on the rainfall, temperature, and relative humidity has been collected on the island. The usually well-marked wet and dry seasons are shown clearly by the average monthly rainfall totals recorded on the island since 1925 (fig. 1). Figure 2 shows the variability of the annual rainfall totals, expressed as departure from the 35-year average of 107.4 inches. Unusually dry periods of about two years are separated by wetter periods lasting about four.

Hygrothermograph stations were established in the forest at three different elevations (approximately 100, 300, and 500 ft) by Dr. Charles Bennett of the Department of Geography, University of California, Los Angeles, in August, 1958; more or less continuous records were obtained until December, 1959. The instru-

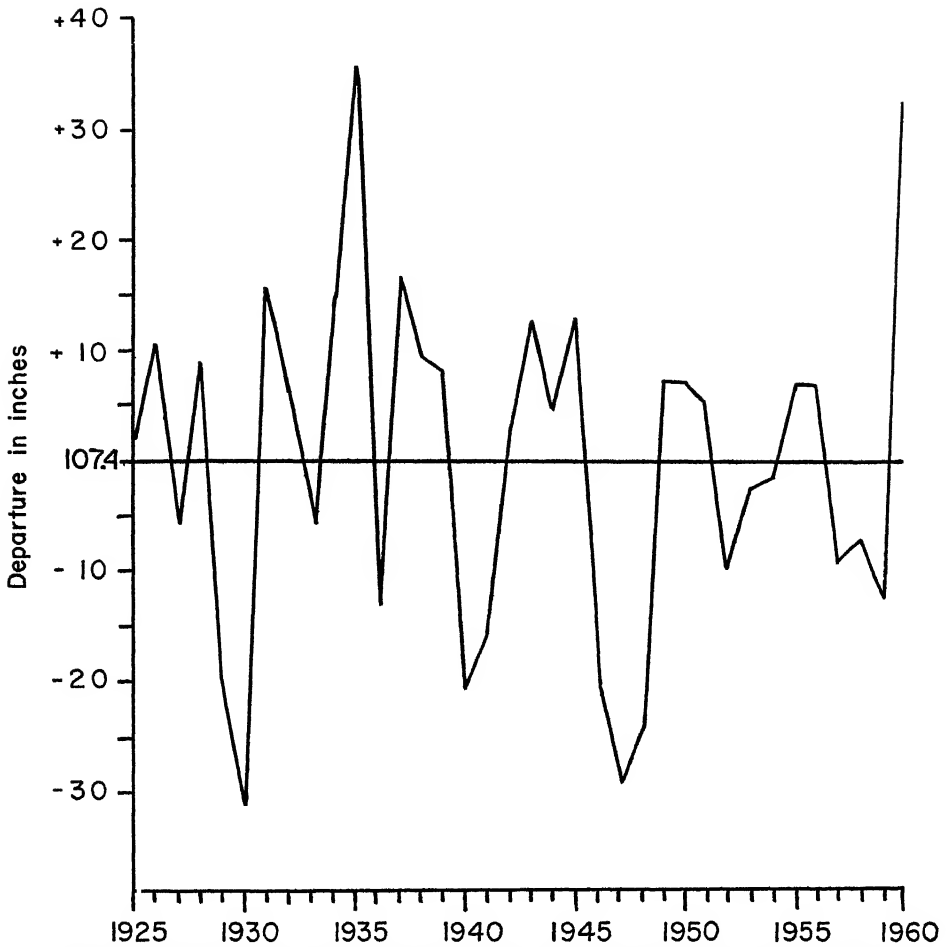


Fig. 2. Rainfall, Barro Colorado Island. Annual departures from the 35 year average of 107.4 inches.

ments were suspended at three different levels at each station. My brief scanning of the records obtained near ground level yielded the following generalizations:

RELATIVE HUMIDITY

Dry Season 50-90 per cent, with extremes of 40-100 per cent.

Wet Season 95-100 per cent, with extremes of 70-100 per cent.

TEMPERATURE

Dry Season 75-85°F, with extremes of 70-90°F.

Wet Season 75-85°F, with extremes of 70-90°F.

The highest temperatures and lowest relative humidities were usually recorded around 1200, and the highest relative humidities from about 0600 to 0800. The temperature fluctuated slightly less during the wet season than during the dry season, and the major temperature differences were between night and day rather than between seasons. Dr. Bennett is analyzing these records in detail and plans to publish them later. Meanwhile, he has kindly permitted me to summarize his data in this crude fashion.

Flora.—Standley (1933) listed 1,259 species of plants from Barro Colorado, of which all but 190 are spermatophytes. The island is completely forested except for a few acres of clearing around the laboratory, but the canopy is broken by the frequent fall of large trees and by the less frequent but far more drastic mud slips. When a large tree falls, it usually takes with it other trees and a tangle of vines, leaving a gap in the canopy and a jumble of tree trunks, branches, and vines on the ground (pl. 3). These areas will be referred to as "blowdowns," though they may be caused by a variety of factors other than wind. After four days of steady rain in December, 1959, several hillside areas of up to an acre each were denuded by mud slips; these were the most severe slips known to have occurred on the island since the lake was formed.

Kenoyer (1929) described the forest on the western half of the island as mature, the rest being in various stages of succession, but thirty years have had an appreciable effect on the less mature areas. Now the dense, sometimes impenetrable second growth which corresponds to the popular conception of "jungle" is found only at the edges of clearings and blowdowns and on the lake shore. Except for blowdowns and large patches of piñuela (*Ananas magdalanæ*), the forest is relatively clear of undergrowth, and I had no difficulty in following wild coatis without the aid of a machete (pl. 2).

Fauna.—The list of animal species known to occur on Barro Colorado continues to grow, but little is known about the biology of most of them. A very few careful studies have been made (Schneirla, 1933, on army ants; Van Tyne, 1929, on toucans; Carpenter, 1934, on howler monkeys), but these are rare exceptions among an endless array of surveys and casual observations. General information on the ecological distribution of animals on Barro Colorado was presented by Allee (1926b), and Allee and Torvik (1927). A collection of samples of the litter fauna was described by Williams (1941).

Not even a good taxonomic list is available for all groups among the vertebrates; reliable, detailed life history, behavioral, and ecological data are almost nonexistent. The 22 species of fish known from the island were listed by Breder (1944), and Dunn (1931) listed 33 species of amphibians. There is no published list of the reptiles, but over 60 species have been recorded. Eisenmann (1952) listed 306 species of birds, and the list is still growing. Over 70 species of mammals have been listed for the island so far, and life history notes on many of them were given by Enders (1935).

TECHNIQUES

Direct observation of free-living wild animals provided almost all that was learned about coatis in this study; five bands that were each followed closely for periods of up to nine months provided most of the data. Intensive observations of bands and solitary males were made, totaling 1,370 hours. This does not include many uneventful hours spent watching roost trees after the coatis settled down at night or before they descended in the morning. In addition, over 450 brief observations were made throughout the island.

Nineteen coatis representing all sex and age groups were kept in captivity for varying periods of time, some for as long as twenty-three months (pl. 4). In addi-

tion, two litters were born in captivity. Live-traps were used both to secure captives and to catch selected individuals for marking with bleach for field identification. Regular commercial hair bleach (Roux) with booster powder added was scrubbed into the fur with a tooth brush to produce a conspicuous pale yellow patch that lasted for several months (pl. 4).

FOLLOWING BANDS

The technique of following selected wild bands of coatis was preceded by observations from blinds set up at food stations. Bananas and bread were placed near a blind in the forest on July 19, 1958, and intensive observations were begun after a band was first seen there on August 3. From the first day, these coatis (Band 1) were well aware of my presence and frequently investigated the blind, coming to within two feet of the front and four feet of the open back. Four days later one came inside the blind and took food from my hand; three days after that I moved outside to feed them. They became increasingly tolerant of my presence, feeding from my hand but not permitting me to touch them. Two weeks later I began trying to follow them away from the food station. The distance and time increased with each trial, and by September 13 I was able to follow them all day.

On August 21 I set up a food station and blind in another area, and soon had another band (Band 2) feeding there. But after twenty-five days they were still too wary of my presence to be followed, and I gave up. Another band (Band 3) had been seen several times in the vicinity of a large natural fruit crop (*Spondias mombin*), and on September 24 a female and her two young came up to me and accepted food. No blind or artificial food station was ever used with this band, but by October 5 I was able to follow them easily. Bands 1 and 3 were watched alternately for the remainder of the first year of the study, when contact was lost with the survivors of both.

Several food stations were established in other areas in September, 1959, and contact was made with two more bands. These were watched originally from blinds, but within two weeks of the initial contacts both bands could be followed at will. Band 4 was followed intact for the remainder of the study; Band 5 was small to begin with, soon dwindled even more, and I stopped observing it in January, 1960.

A very small band consisting of two adult females and two juveniles (Band 6) was seen frequently near the laboratory clearing during the second year of the study. It was live-trapped intact in December, 1959, and kept in captivity. Both of the litters born in captivity came from these two females.

After an interval of several days, a band could be picked up again at the food station, at a currently favored fruit tree, or by systematic searching of the home range. This last method was used exclusively for Band 3 and depended to a large extent on conditioning the coatis to come for food, or at least not to run off, when I called to them. They often recognized my call, apparently before they had identified me by sight or smell, and immediately ran toward me. This positive response to my calls was also very helpful in maintaining contact with the bands in their daily rambles through the forest. The relative tameness of the individual coatis varied greatly; some could eventually be handled to a limited degree, while others were always wary and never came closer than a few yards. This technique

never worked well with adult males, and most of the data on them were collected from briefer individual observations, from blinds, and from extended observations while they were with the bands.

ADVANTAGES

The advantages of such a close relationship between the observer and the animals being studied are obvious; many details of the life history and social behavior could be obtained in no other way. Home ranges can be mapped directly, and reliable information gained on the details of daily movements and differential use of the range. Continuous records provide quantitative data on activity patterns and on the use of specific places for sleeping and rearing the young. Direct observation reveals details about food habits that cannot be gained from stomach content and scat analysis. Many interspecific relations can be observed, and the intra-specific social relations can be studied in detail in the animals' natural environment. Dissection of specimens can tell us much about what an animal is capable of doing at any given time, but just what it actually does, and how, can be learned only from observations in the natural habitat. Simultaneous observations of captive and wild coatis brought home time and time again the fallacies and distortions that may arise from a study of animal behavior based entirely on captives in an artificial environment.

LIMITATIONS

Although most of the information gained by this technique can be obtained in no other way, a constant watch must be kept for distortions in the normal pattern caused by the observer's presence. All of the observations must be carefully interpreted, and full use must be made of all opportunities to check their validity by comparing the results obtained under different conditions. Furthermore, almost constant contact must be maintained with each band if one is to be present when important developments occur—developments that may come only once in a year. Particularly in a study such as this one, where conditions cannot be controlled and may vary tremendously from place to place and time to time, there is a great danger of attaching too much importance to any set of figures. Numbers in such a situation should not be regarded as defining with magical precision and accuracy the functioning of living organisms. An impressive set of figures can precisely represent a false situation as well as a true one, and I have discarded some interesting counts because I knew that the information they conveyed about certain behavior patterns was distorted. "Objective" data on behavior must necessarily be based on very subjective knowledge and decisions, and I have not hesitated to use admittedly inconclusive subjective data where I felt they were the most accurate.

Such words as "often," "frequently," "probably," and "apparently" find constant use throughout this report. Coatis are not machines; they are living organisms in a complex environment, and their activities are marked by infinite variety. Furthermore, no one has yet found a way to enter the mind of another individual and to know what actually goes on there. We can only describe that individual's actions and what seem to be relevant environmental conditions as best we can, with full knowledge that our estimate of what is relevant may miss the mark completely.

TERMS AND CODE NAMES

The following age classification is used in this report:

1) Juveniles or young: animals not yet fully grown (full growth is reached at approximately the 15th month).

2) Subadults: animals fully grown but not sexually mature. Males are arbitrarily called subadult until their testes descend at about the 24th to 25th month. Females may or may not breed during their second year, and are arbitrarily called subadult until January 1 of their second year (about their 20th month).

3) Adults: males whose testes have descended (males normally become solitary at this time); females after January 1 of their second year (the approximate beginning of the breeding season).

"Breeding season" refers to the six months from the onset of mating until the new young are about two months old, when their care no longer requires major modifications of the band's daily routine. The dry season coincides approximately with the first few months of the breeding season.

The code names of the coatis I could identify individually are based on the following system:

1) The bands I watched closely are numbered 1 to 6 in the order in which I first made contact.

2) Members of bands are designated by M or F (for male and female), plus a number. The first digit indicates the band, the second the individual animal. Capital M or F indicates that the animal is adult or subadult; small m or f is used for juveniles.

Examples: f45 = juvenile female 5 in Band 4. (At the end of her first year a capital F replaces the small f.) M13 = yearling male 3 in Band 1.

3) Solitary males (females) are designated MS (FS), plus a small letter for each individual. Example: MSc = solitary adult male c.

4) All captive animals have a capital C before their regular designation during their period of captivity. Captives whose origin was uncertain are simply designated CM, Cm, CF, or Cf, plus a small letter for each individual of each sex.

Examples: CMSb = solitary adult male b, while in captivity. CF61 = adult female 1 of Band 6, while in captivity. Cmd = captive juvenile male d.

DAILY ACTIVITY PATTERNS AND INDIVIDUAL BEHAVIOR

DIURNAL PATTERN

The coatis on Barro Colorado are strongly diurnal. The bands are active during most or all of the daylight hours, and retire at night to roost trees within their home ranges. Solitary males tend to follow the same routine, but they are frequently seen abroad during the night. In my two years on Barro Colorado no females or young were seen active at night outside of the mating period, with the exception of one injured female that left her band and came into the clearing for food. I was able to keep continuous contact with the semitamed bands for several consecutive days by following them to their roost tree in the evening and meeting them there on their descent the next morning. The bands generally descend from a

roost tree in the half-hour preceding sunrise and ascend a roost tree within the hour following sunset (fig. 3).

The official sunrise and sunset times used in figure 3 are those for the Canal Zone town of Cristobal, fifteen miles northwest of Barro Colorado; the corresponding times for Barro Colorado are less than one minute earlier. The light on the

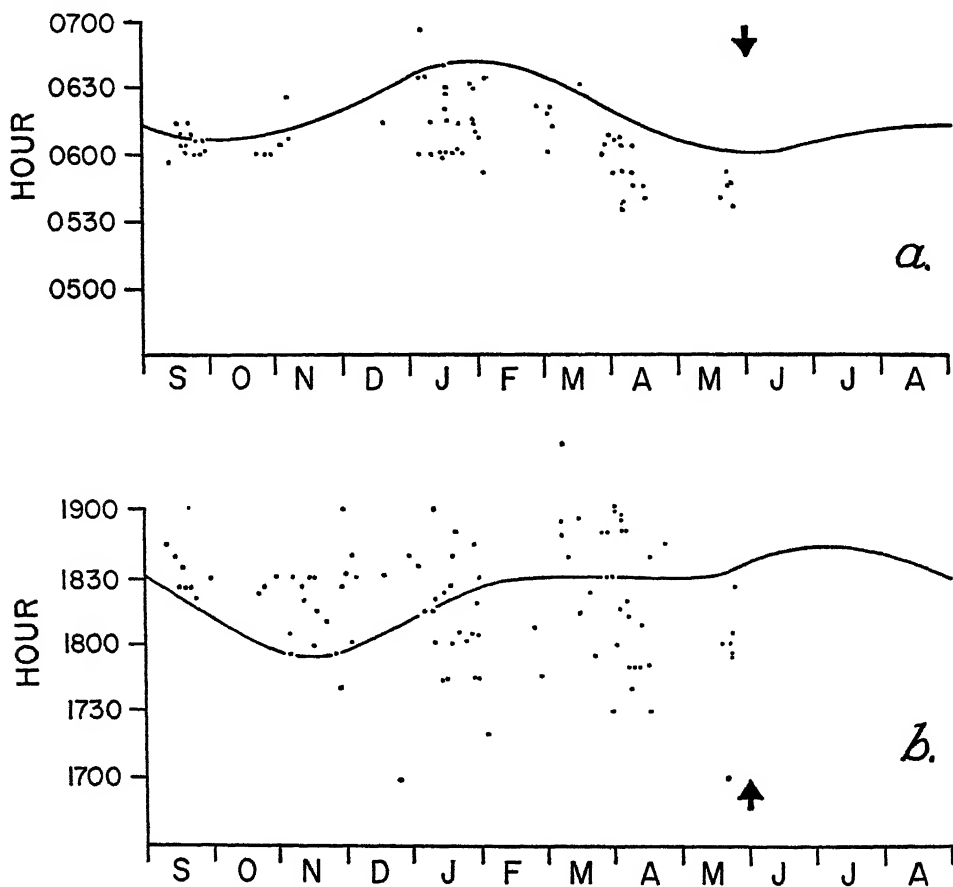


Fig. 3. *a.* Time of descent from roost trees. The heavy line is the sunrise curve; no data are available for the months to the right of the arrow. *b.* Time of ascent into roost trees. The heavy line is the sunset curve; no data are available for the months to the right of the arrow. Mating activity occurred from January to April; the early ascent times in May were correlated with the presence of new young.

forest floor was just strong enough for me to follow the coatis without a flashlight in the half-hour before sunrise and the half-hour after sunset. But details of local weather, exposure, and topography affect the actual light intensity perceived by the coatis at these times.

Ascent and descent are of course not equivalent to going to sleep and waking up. Because of the poor light and the usually dense crowns of the roost trees, it was frequently impossible to tell these latter times exactly, especially in the evening. Sometimes, if the ascent is late, the coatis settle down immediately; but if

the ascent is early, a period of mixed rest, self and mutual grooming, and climbing around to new positions may last until dark or after. Ascent is occasionally as much as an hour or two before the usual time for retiring.

In the morning before descent there is usually a period of self grooming, urinating, and defecating which lasts about ten or fifteen minutes, but the descent is much more regular with respect to the sun than is the ascent. On several occasions the descent was delayed, apparently because the coatis were alarmed by my presence. They remained in the tree watching me, and on three occasions descended by a route which brought them to the ground thirty to fifty feet from where I was waiting at their usual point of descent. One unfamiliar solitary male lay watching me from a branch at the top of the descent route for thirty minutes until I left.

Occasionally ascent of the roost tree in the evening is delayed while the coatis take advantage of a particular food source. For example, on November 29, 1958, Band 3 climbed a large fig tree to feed at 1815. Sunset was at 1757, and I would have expected them to retire at about 1830. The band remained in the tree feeding until 1835. Two juveniles that did not ascend with the band settled down at 1830 between the buttresses of a nearby tree as if to sleep. The only adult female that was with the band grunted softly when she reached the ground, and the two juveniles joined the rest of the band under the fig tree. The whole band then moved off to a roost tree three hundred meters distant, ascending at 1900. Other delays of this type were also observed, including some due to artificial feeding of the coatis around the laboratory clearing until after dark.

Major deviations from the nonbreeding activity cycle are apparent during the mating period, the period of late pregnancy, and during the first month after the young are born. Some of these deviations are simply changes in the times of ascent or descent associated with such activities as nest building, but others, such as the relatively early waking times during the mating period, are harder to explain. In the mating period the coatis tend to go into the roost trees earlier with respect to sunset, and to descend earlier in the morning. This period is also characterized by increased nocturnal activity among both band members and adult males, and by more resting during the day. Females in the last week to ten days of pregnancy often ascend their roost trees over an hour early to work on nests. After the young are born and on the ground, the whole band goes into the roost trees early, but descends shortly before sunrise.

ROOST TREES

Of the 130 coati sleeping places I observed, all but 8 were in trees. Band 3 accounted for all 8 exceptions, which represent 25 per cent of the sleeping places observed for that band. Seven nights were spent on the ground between the buttresses of large trees (4 different locations), and one was spent on an exposed slanting log 4 feet above the ground.

The trees chosen for roosts are usually medium to large, with fairly dense crowns and with good access routes via lianas and/or saplings. The same route is commonly used each time the coatis ascend or descend, and may be quite complicated. Of the 50 different locations where coatis slept, 30 (60 per cent) were on ridges or on the edges of large ravines, 13 (26 per cent) were on hillsides well up from the bottom,

3 (6 per cent) were near the bottom of hillsides or ravines, and 4 (8 per cent) were on fairly level ground.

The coatis usually sleep well up in the crown of the roost tree. They may stretch out on a large limb or curl up in a crotch, and they frequently take advantage of natural platforms formed by dense tangles of limbs and vines. The whole band usually sleeps in a fairly restricted area of the crown. Captive coatis of mixed sexes and ages slept curled up together, often on top of each other, inside or on top of a large packing crate.

During the breeding season, tree nests are often built by bands and by adult males, both for sleeping and for resting during the day. However, their primary use is for holding the new young for the first few weeks after they are born.

The locations of the known roost trees for Bands 1, 3, and 4 are shown on the home range maps (page 169), and their chronological use is summarized in table 1. Many of those trees I saw occupied only once, and there were undoubtedly many others that I never saw. None of the trees was used for many nights in succession, but some (2 and 3 for Band 1; 4 for Band 3; and 2 for Band 4) were frequented repeatedly over a period of months. Sometimes favored trees were abandoned for others only a few meters away. Roost 2 for Band 1 (near the laboratory clearing) was also used by numerous other coatis, including both other bands and solitary males, often on the same nights. Some roosts were occupied frequently while a good fruit crop was nearby, but otherwise were seldom used (6 and 8 for Band 4). Roost 2 was used especially often by Band 4 while an adjacent *Chrysophyllum panamense* tree was in fruit (January 28 to February 3), and the band went directly into the fruit tree to feed before descending in the mornings.

DAYTIME REST

The coatis spend almost all of the twelve daylight hours wandering about searching for food, but they stop occasionally for brief periods of self and mutual grooming, and may extend these pauses to include a rest period. Simple grooming sessions may last only a few minutes, but up to two hours or more may be spent dozing on the ground (rarely), on fallen tree trunks, or up in vines or branches of standing trees (pl. 5). The rest periods usually start and end with grooming, or a band may spend up to an hour in a session of mutual grooming, self grooming, "play" by the juveniles and subadults, sunning, and dozing—all going on simultaneously and alternately among the various members. Sleeping positions in the day are similar to those used at night: the coatis curl up on the ground or on sufficiently broad logs or limbs, or stretch out, often with the chin resting on the front paws. When curled up, they often wrap their tails around in front of their faces, and young animals especially may put their front paws over their noses. Frequently several animals will sleep partly on top of each other. Rest periods may occur during any of the daylight hours, but are more common in the late morning and early afternoon (fig. 4). Except when new young are present, the bands show the same general pattern of rest periods throughout the year, although the total time spent resting varies considerably between the wet and dry seasons (fig. 5). The rest periods observed during the four and one-half days just after Band 4's new young became

TABLE 1
CHRONOLOGICAL USE OF ROOST TREES BY BANDS 1, 3, AND 4
(Numbers of roost trees refer to those on the home range maps, figs. 11, 12, 13;
the roost trees for each band are numbered separately.)

Band 1		Band 3		Band 4	
Date	Roost	Date	Roost	Date	Roost
1958				1959	
Sept. 9.....	1	Sept. 17.....	?	Nov. 4.....	1
Sept. 13.....	1, 3 ^a	Sept. 18.....	?	Nov. 5.....	1
Sept. 15.....	2	Sept. 19.....	?	Nov. 16.....	2
Sept. 16.....	3	Sept. 22.....	?	Dec. 2.....	3
Sept. 17.....	3 ^a	Oct. 5.....	1	1960	
Sept. 18.....	3	Oct. 23.....	2 ^c	Jan. 4.....	4 ^x
Sept. 19.....	2 ^a	Oct. 24.....	2 ^{a, c}	Jan. 5.....	5 ^x
Sept. 22.....	3	Oct. 27.....	3	Jan. 6.....	6 ^x
Sept. 23.....	2	Oct. 31.....	2 ^{a, o}	Jan. 8.....	7 ^{a, x}
Sept. 24.....	4	Nov. 1.....	3 ^a	Jan. 9.....	6 ^x
Sept. 26.....	3	Nov. 5.....	2 ^{a, o}	Jan. 10.....	6
Oct. 21.....	5	Nov. 6.....	4 ^c	Jan. 13.....	6 ^x
Oct. 26.....	2 ^a	Nov. 10.....	8	Jan. 14.....	6
Nov. 17.....	6	Nov. 11.....	1	Jan. 15.....	8, 9 ^b
Nov. 21.....	6	Nov. 14.....	6 ^a	Jan. 16.....	5 ^x
Dec. 3.....	7	Nov. 15.....	7	Jan. 17.....	8, 9 ^b
		Nov. 20.....	7	Jan. 20.....	8, 9 ^b
		Nov. 24.....	5	Jan. 22.....	8 ^x
		Nov. 29.....	7	Jan. 27.....	10 ^x
		Dec. 4.....	8 ^a	Jan. 28.....	2 ^x
		Dec. 18.....	9 ^a	Jan. 29.....	2 ^x
		Dec. 29.....	10	Feb. 1.....	2 ^x
				Feb. 2.....	1
				Feb. 3.....	2
				Feb. 24.....	11
				Feb. 25.....	7
				Mar. 19.....	12
				Mar. 22.....	8
				Mar. 30.....	2 ^a
				Mar. 31.....	7 ^a
				Apr. 1.....	13 ⁱ
				Apr. 2.....	13 ⁱ
				Apr. 3.....	13 ⁱ
				Apr. 4.....	14 ⁱ
				Apr. 5.....	13 ⁱ
				Apr. 6.....	15 ⁱ
				Apr. 7.....	14 ⁱ
				Apr. 8.....	14 ⁱ
				Apr. 9.....	14 ⁱ
				Apr. 10.....	14 ⁱ , 16 ^k , 17 ⁱ
				May 19.....	
				May 20.....	4
				May 22.....	18
				May 23.....	2
				May 24.....	19, 20 ^a
1959		1959			
Mar. 6.....	2	Jan. 3.....	11		
Mar. 30.....	2	Jan. 17.....	12 ^d		
Mar. 31.....	7	Jan. 19.....	13 ^c		
Apr. 6.....	3	Jan. 27.....	14 ^a		
Apr. 7.....	2	Jan. 30.....	14 ^{a, c}		
Apr. 15.....	8	Mar. 9.....	1		
Apr. 16.....	9	Mar. 14.....	3		
Apr. 25.....	3 ^a	Mar. 15.....	15 ^f		
May 18.....	10 ^b	Mar. 25.....	3		
Aug. 8.....	11	Mar. 26.....	16		
		Mar. 27.....	3		
		Apr. 3.....	3		
		Apr. 4.....	8		

^a Part of band only.

^b M13 only.

^c Slept on ground between buttresses.

^d M31 only.

^e Slept in tree (on ground here January 30).

^f Slept on log four feet above ground.

^g Adult male slept in same tree with band, during mating period.

^h MSf only (in tree near band).

ⁱ F42 only, in late pregnancy.

^j F42 and her new litter.

^k F41 and her new litter.

^l F43 and her new litter.

active on the ground were fairly evenly spread over all of the daylight hours (fig. 9).

The following discussion of seasonal variation in daytime resting habits is based on table 2. In the wet season rest periods are short and infrequent. The coatis rested during only 1 per cent of the 3,838 coati-hours of wet season observations. More frequent and longer rest periods in the dry season accounted for 14 per cent of the coati-hours during which bands and adult males were observed. Increased rest in the dry season is presumably made possible by the availability of large fruit crops, which eliminate the necessity for continuous searching for small litter animals.

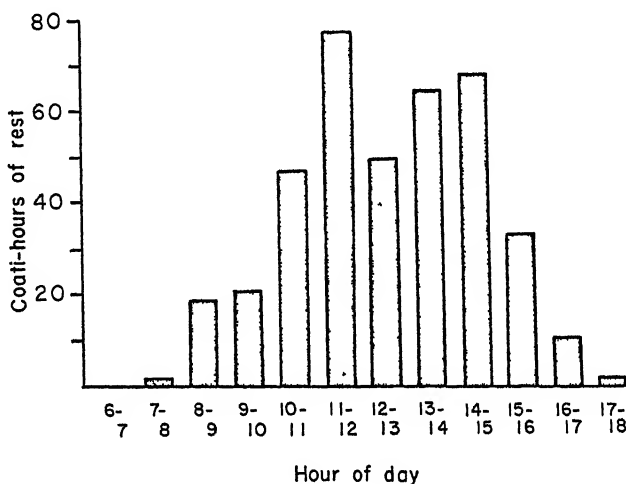


Fig. 4. Hourly distribution of daytime rest periods. All observations are included except those for Band 4 after April 9, 1960, when the young were born (see fig. 9). Adjustment has been made for differences in amount of observation in each hourly period. Coati-hours equals the hours of each observation times the number of coatis present.

The mating period of the Barro Colorado coatis occupies approximately one month early in the dry season. Changes in band activity during the mating period (frequent presence of adult males and increased nocturnal activity and intra-specific strife) did not greatly affect the pattern of daytime rest. Bands 1 and 4 both had mating periods during which they were joined by an adult male, but Band 1's male was less often present and none of the females bore young. Both bands rested the same proportion of the time in the mating period whether the adult male was present or not, and Band 1 rested as much during the mating period as it did during the remainder of the dry season. Band 4, however, rested twice as much after the mating period as they did during it. Two facts may account for this apparent increase: the mutual grooming sessions (which are much more frequent during the mating period) are not included in the totals for rest, though they also function as such; and all four adult females were pregnant. The resting percentage for F42 during her last eight days of pregnancy (after the band had dispersed) is

about the same as that for the whole band during February and March. She also spent about 10 per cent of her daylight hours building nests.

Band 3, with only one adult female, was not joined by an adult male and exhibited no change in activity in the dry season.

LOCOMOTION

Coatis spend most of their active hours on the ground, but their excellent climbing ability is well known. Some writers have even gone so far as to say that coatis are chiefly or largely arboreal (Elliot, 1904; Goldman, 1920). The ones I watched on

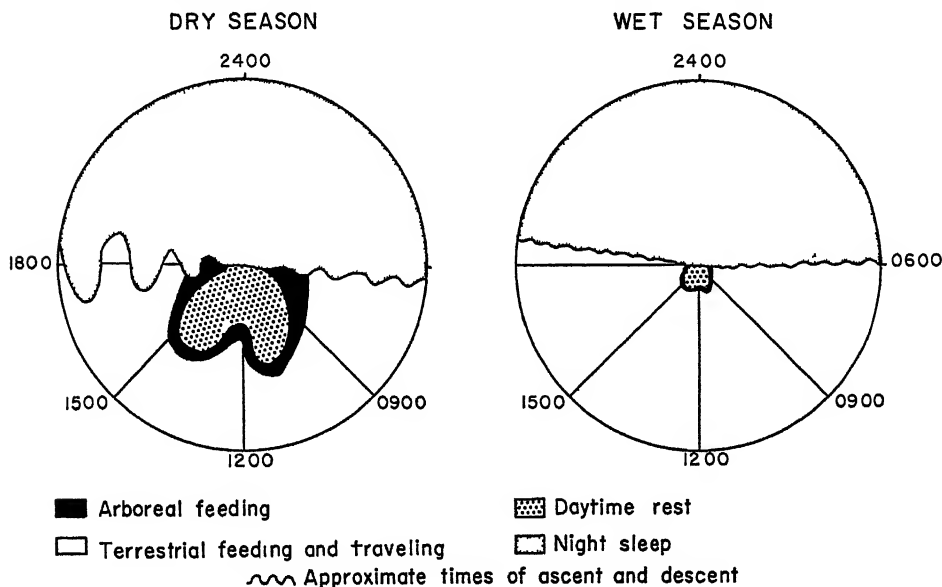


Fig. 5. Summary of 24-hour cycles of activity of coatis in Bands 1, 3, 4, and 5. The area covered by each pattern represents the percentage of time spent on that activity. "Night sleep" includes nocturnal activity in the mating period. The dry season records for Band 4 are not included after April 9, 1960, when the young were born.

Barro Colorado were in trees only 3.5 per cent of their total active time, i.e., feeding time, and about 90 per cent of this arboreal feeding occurred in the dry season. Since coatis are more conspicuous in trees, especially around the clearing in the dry season, the 3.5 per cent figure may be slightly higher than it should be. However, their preference for trees as daytime resting places, as night roosts, and as birthplaces and nurseries for the young results in these coatis spending over half their lives in trees.

Walking and running.—On the ground and on horizontal tree trunks and branches, coatis walk with the same pattern of limb movements employed by most of the Carnivora. The four legs are moved singly in a diagonal pattern: left forefoot, right hindfoot, right forefoot, left hindfoot, etc. At slow speeds, the body is always supported by three legs. With further acceleration the coati shifts almost immediately to a rocking gallop, with both forefeet moving simultaneously, followed by both hind feet. As the hind feet come forward, the back is strongly arched.

TABLE 2
PERCENTAGE OF DAYLIGHT HOURS SPENT RESTING IN WET AND DRY SEASONS

Band	Period	Adult male	Total coati-hours	Coati-hours resting	Per cent
WET SEASON					
1, 3, 4, 5	3,838	44	1
DRY SEASON					
1, 4	Mating period	1,668	201	12
1, 3, 4	Outside of mating period	1,492	231	15
	Total or average.....	3,160	432	14
1	Mating period ^a	Present	150	25	17
		Absent	139	24	17
	Total or average.....	289	49	17
	Outside of mating period...	562	101	18
4	Mating period ^b	Present	1,229	136	11
		Absent	150	16	11
	Total or average.....	1,379	152	11
	Outside of mating period...	380	87	23
(F42) ^c	(Late pregnancy).....	(106)	(23)	(22)
3	Dry season ^d (no mating period)	550	43	8

^a Band 1 mating period from February 25 to March 15, 1959.

^b Band 4 mating period from January 4 to February 4, 1960.

^c F42 observed from April 2 to April 9, 1960. The figures are included in those for Band 4 as a whole.

^d Band 3 observed from January 1 to April 11, 1959.

An adult male in full gallop was clocked on an automobile speedometer at 17 miles per hour by Mr. Phillip Welles, Superintendent of the Coronado National Monument (personal communication, 1960). Goodwin (1934) noted that coatis driven by hounds often run for as much as three hours before taking to trees.

Climbing.—The basic patterns of either walking or galloping are used in climbing, depending on the character of the stem being climbed. The coati's feet are plantigrade and armed with strong claws on each of the five toes. The claws on the hind feet are sharper and more strongly curved than those on the front feet, and are more important in climbing, particularly in vertical descents.

When ascending vertical vines or trunks up to about two inches in diameter, coatis "walk" up with the alternate, diagonal pattern of leg movement. The stem is grasped "hand-over-hand" between the forepaws, while the hind feet are placed more nearly on the front of the stem. Coatis "gallop" up vertical stems with diameters of about three inches or more with the front legs spread in a grasping manner

and the hind feet flat on the stem. When the stem is between two and three inches in diameter, or is at an angle less than vertical, coatis use a mixture of the two modes, tending to "walk" whenever possible, especially where projections can be grasped by the front paws.

The same general rules apply to the descent, which is almost always head first. (On several occasions I saw coatis slide down backwards when they were only two to four feet from the ground.) The hind feet grasp the stem and are turned back and up, as in tree squirrels, to get the maximum support from the hind claws (fig. 6). On small stems the front feet alternately grasp and are then placed flat, whereas large trunks are grasped by both the fore and hind feet with the legs spread wide in a tight clasp. Large trees are descended with great care, and a change is made to smaller saplings or vines whenever possible. In fact, large trees are never descended directly if vines or saplings can be used, or a crossing can be made to an adjacent tree with a thinner trunk.

Coatis frequently hang upside down, suspended by all four feet, to feed along the underside of horizontal branches, vines, and small suspended logs. They also "walk" suspended below lianas, especially where the footing is insecure or when they lose their balance.

The principal function of the long tail is to provide balance when the coatis are traveling on lianas or branches, and it is swung from side to side as the animals make horizontal crossings. Ingles (1957) stated that the tail is "almost prehensile" when a coati descends lianas, branches, or small trunks at a steep angle, and is curved around the stem and pressed tightly against it, acting as a brake. In two years I saw this perhaps twice—almost invariably the tail trailed out behind without touching the stem (fig. 6). Chapman (1938) used bananas to induce an adult male to walk both tight and slack wires, and commented on the use of the tail as a balancing rod. This same male once stood erect on his hind legs on the tip of a slender inclined pole.

Coatis climb more deliberately than such arboreal artists as the tree squirrels (*Sciurus*) and white-faced monkeys (*Cebus*), but often less deliberately than the howler monkeys (*Alouatta*), which have an advantage over coatis in the use of a prehensile tail. Usually coatis avoid making limb-to-limb leaps of more than about three feet, but they do not hesitate to jump much farther when pressed. A small juvenile I tried to capture in a sapling jumped fifteen feet to the ground and escaped.

Azara (1838) first noted that coatis often turn by raising the forepaws and whirling around on the hind feet. Seton (1926) commented that this habit is correlated with the precarious footing in trees, and is shared with other animals which have to turn in close quarters, such as the mountain goat.

Tree-to-tree crossings at any height are made constantly, and sometimes these are rather precarious. Several times I observed an adult male crossing with great care from a large fig tree to an almendro tree in fruit more than a hundred feet above the ground. After he had crept to the slender tip of a small branch of the fig and reached out with his forepaws to grasp the nearby tip of an almendro branch, he let go with his hind feet and swung and scrambled up onto the almendro branch. This method was also used by other individuals at various times. One



Fig. 6. Coati descending vertical trunk. Note hind feet turned back and up and tail out free behind. Drawn by Gene M. Christman from a photograph by the author.

complex access route to a large roost tree used by Band 4 included a jump of about four feet across and down from the limb of an adjacent tree to the roost tree. The four full-grown females made this without difficulty, but the three juveniles showed great reluctance to jump. After much running back and forth and preliminary crouching, two finally made the leap successfully. The third continued to look for a less risky way over until it had worked its way down almost to the ground and was able to transfer to a liana hanging from the roost tree.

Occasionally coatis fall from considerable heights. During the 1960 mating season, I witnessed a fight between two adult males in which the younger male fell forty feet from the branch on which he was attacked. He was apparently unhurt, because when the older male had raced down the tree and reached the spot a few seconds later, the fallen coati was already in flight. On the night when Band 3 fed in a fig tree until after dark, a juvenile fell from a height of at least thirty or forty feet during the descent, and landed at my feet with a thud after crashing through the flimsy fronds of a small palm about ten feet from the ground. She picked herself up immediately and showed no ill effects.

Swimming.—Coatis are capable swimmers when the need arises, paddling along with their snouts curled up like miniature snorkels; however, I never saw a coati enter deep water voluntarily.

INVESTIGATIVE AND ALARM REACTIONS

Investigation.—The coatis on Barro Colorado are not very alert, and an observer can often approach quite close to an individual or band without drawing its attention. I once stood very still in the path of an advancing band I had never seen before, and one coati fed along, nose in the litter, to within a foot of me before it noticed me and jumped back with a surprised bark. At other times individuals in bands noticed me when I was standing still or moving very slowly and carefully at distances of from 10 to 75 feet. Coatis feeding near blinds soon became aware of my presence and displayed much interest. Coatis that I was observing occasionally directed their attention to other animals, to inanimate objects moving in the wind, to objects not in sight but presumably smelled by the coatis, and to some types of sounds heard in the distance.

Definite patterns of investigative behavior are used in all such situations when the object of interest has not been satisfactorily identified. The coati turns its head toward the object in question, curls up its snout and sniffs repeatedly, and often bobs its head up and down. One or both of the ears may also be rotated forward. Often, especially if the object of interest has already been sighted, the coati will rear up on its hind legs with the front legs dangling down or slightly out to the sides. The distance receptors are thus elevated above some of the intervening low plant growth. This upright investigative posture is also typical of raccoons, kinkajous, and olingos (*Bassaricyon gabbii*).

The head-bobbing may serve three functions. An object seen against a confusing background, such as the tropical forest, can be seen more clearly if the head is moved so that the object seems to move against the background—a device I found helpful on many occasions. Also, moving the head may aid in sound location. Finally, by bobbing their heads, coatis are able to sample more of the air with their

noses, and they are able to locate specific objects using only their olfactory sense (unseen food objects are commonly located in this way). The occasional sight of this action being performed with the eyes half closed and the nose actively twitching is an indication that head-bobbing is at least partly an aid to olfaction.

Nearby objects with which a coati is unfamiliar are investigated cautiously, with the body and snout stretched out in a straight line to their fullest extent. The tail is usually extended straight out behind, but may be held in a vertical position (pl. 7). The coati, sniffing continuously, inches tautly forward, prepared for a quick leap backwards at the slightest disturbance.

Single coatis or small groups that are accidentally separated from the band sometimes follow, nose down, the exact route taken by the others, obviously guided by the scent trail. However, if such a trail is not recent and fairly direct, it can be very difficult to follow owing to the tortuous, criss-crossed meanderings of the scattered individuals. Faced with this problem, the searching coatis often run in a series of loops through the home range until they locate the others of the band by smell, sound, or sight. They give vocal signals (chittering) during the search and keep their noses to the ground much of the time. Visual searching seems to play a lesser part, and they sometimes come within plain view of the others without noticing them. The searching of adult females is relatively deliberate, of subadults more "nervous" with more running and chittering, and of juveniles often panicky.

I have seen coatis respond to sounds and smells which I could not detect, and they have sufficiently good night vision to move easily through the forest, and even to climb trees, when a man can see nothing.

These observations, together with those on the use of smell and sight for locating food (page 184) and the roles of the distance receptors in communication, indicate that coatis rely most heavily on their highly developed olfactory sense for gathering information from the environment, somewhat less on hearing, and perhaps least on vision.

Alarm.—After an unknown situation or object has been investigated, the coati either resumes its normal activity or reacts with alarm. An alarm reaction may also be performed without previous investigation in response to a sudden stimulus, such as a loud noise or a quick movement. The stimuli which elicit alarm behavior are both varied and variable—from time to time and from animal to animal. They include surprisingly innocuous but apparently unfamiliar objects, such as small turtles (see page 165). Sudden movements and loud noises: the sight or sound of a running animal; alarm calls of birds or other mammals, such as agoutis; and loud barks or coughs from unseen animals almost invariably cause alarm. But coatis usually ignore such common loud noises as claps of thunder, the crash of falling trees, and the roar of nearby howler monkeys. The sight, sound, or smell of a human may cause alarm, but the reaction is not intense if the person remains motionless and quiet. Alarm behavior observed when there was no apparent cause was presumed to be the result of disturbing olfactory or auditory stimuli, possibly the sound or smell of unseen predators.

When the location of the source of alarm is unknown, the coati ordinarily dashes less than ten feet up a nearby tree (pl. 6). This is an especially common response

to the alarm grunts of another coati. Once up on the tree, the coati may "freeze" for anywhere from a second or so to more than a minute trying to locate the source of the disturbance; as soon as it is located, the coati usually jumps down and runs off. Occasionally coatis on trees will climb when pursued and may make their way through the tree tops for some distance before descending to the ground. But the usual reaction is to descend as quickly as possible, sometimes leaping the last ten or fifteen feet.

A coati suddenly alarmed by a nearby object will usually bark and jump back. This may be followed by panic and flight, or by a short period of alertness and tail-switching and a return to normal activity if the danger is not pressing. If the alarm is neither intense nor sudden, the coati may give a series of grunts and retreat, turning frequently to look back at the source of alarm. Switching the tail jerkily from side to side is common in such situations. If the alarm is intense, a coati may burst into panicky flight, grunting excitedly. These dashes are often short, especially if the cause of alarm is obscure. When a whole band is involved, there is a noisy eruption of wildly scampering coatis, and the next second the forest is as still and quiet as if every coati had vanished. They may be standing or clinging to tree trunks a few feet away, but they go unnoticed, so neatly and quickly is the maneuver performed by the entire band. If no further cause for alarm appears, they soon relax and go about their business. If the alarm continues they may slip quietly off, or they may be flushed into another noisy retreat.

REACTION TO RAIN

It rains almost daily through most of the year on Barro Colorado. Frequent hard downpours interrupt the feeding activities of many animals, and their reactions are sometimes surprisingly vigorous. For instance, every daytime shower is greeted by a full-throated chorus from the howler monkeys.

Light rain scarcely penetrates the canopy. Coatis usually ignore such showers even when they are accompanied by loud thunder, but sometimes react to them by becoming somewhat "nervous," moving about more quickly, and chittering. At such times they tended to run more readily from me, so that I occasionally lost contact. Even if a shower is prolonged or intense enough to penetrate the forest canopy to a moderate extent, all but the juvenile coatis may go about their normal routine with only a slight increase in nervousness. Juveniles usually seek their mothers and stay close even when the mothers do not seem very concerned.

When a hard rain comes through the canopy, the coatis seem very nervous and invariably run for cover. They travel more bunched up than usual, the juveniles staying especially close to their mothers. In one hard shower, F32 ran to cover with her back arched and her two six-month-old young running close beside and behind her with their heads under her belly. Later the same day these three were caught in another downpour, and after abandoning the leaky shelter of a palm clump, the female went into a burrow under the buttresses of a large tree. One juvenile followed, but the other refused to enter and ran around outside in the rain, chittering loudly. The two inside emerged, and all three went back to the palms. Soon the female ran back to the burrow, and again one of her young fol-

lowed while the other ran around the tree in the rain chittering. Finally the other two came back out, and all three huddled among the buttresses until the shower was over.

Shelter may be sought in any of a variety of places: piles of fallen palm fronds, brush piles, blowdowns, piñuela patches, the buttresses of large trees, clumps of small palms, and dense tree tops. Few shelters are really effective in the hardest downpours, and if such rains are prolonged the coatis may change shelters one or more times. Once in the shelter they sit hunched together, with the juveniles close in under their mothers. The females frequently groom the young while waiting out a shower.

As soon as a hard shower lets up so that it is no more than a light rain, the coatis go on about their business. A few hard shakes usually free the fur from most of its water, but after a very hard shower the coats may be soaked and look sleek in places.

GROOMING

Coatis frequently groom themselves with their teeth and claws. Where possible, they scratch vigorously with both front paws in a rapid, alternating motion. However, any foot may be used separately on any part of the body it can reach, and the various positions assumed during scratching are frequently contorted. A scratching coati may lie on its back or side, sit up on its haunches, or stand on three legs while scratching with the fourth (pl. 8). Coatis also use their incisors as pincers, nipping the skin lightly in a very rapid series of bites. Frequently, scratching and biting are employed together on a particularly irritating spot (pl. 7).

This self-grooming is presumably in response to the irritation caused by ticks and other external parasites. I never saw coatis performing the apparently irrelevant grooming so often done by monkeys in situations of frustration or uneasiness. A busily scratching coati often seems oblivious to all else—I once saw a juvenile so engrossed in scratching her abdomen with both front paws that she lost her balance, rolled off a log, and then lay scratching herself on the ground without having missed a stroke.

Mutual grooming is also common.

SOCIAL BEHAVIOR

POPULATION STRUCTURE

COMPOSITION AND STABILITY OF BANDS

Adult female coatis and their young live in bands (pl. 9). The basic unit of organization seems to be the family group of an adult female and her offspring less than two years old. Several such family groups are commonly combined in a single band, which may also include adult females that have no young. Probably most or all of the adult females in a band are closely related, as mothers and daughters, sisters, or cousins. The compositions of the 5 bands that I followed closely are summarized in table 3 for the first date I saw each of them and the last.

From 1958 to 1960 no bands with more than 20 individuals were seen on Barro Colorado. Of the bands that I followed closely, only one had over 10 members.

TABLE 3
COMPOSITION OF BANDS
(Code names for individual coatis are explained on page 103.)

Date	Adult females with young	Adult females without young	Subadult males and females	Subadult, sex not known	Juvenile males and females	Juvenile, sex not known	Total
BAND 1							
Aug. 1958	F10, F11	F12, F13	F14, F15, F16, F17, M11, M12, M13	1	f18 ^a , f19 ^a	1 ^a	15
Aug. 1959	0	F11, F15, F16, F17	F19 ^b	0	0	0	5
BAND 3							
Sept. 1958	F31, F32	0	F33, F34, M31	0	f35 ^a , f36 ^a , f37 ^d , m32 ^d	0	9
April 1959	0	F34	M31	0	0	0	2
BAND 4							
Oct. 1959	F41	F42, F43	F44	0	f45 ^a , f46 ^a , m41 ^a	0	7
June 1960	F41, F42, F43, F44	0	F45, F46, M41	0	0	8	15
BAND 5							
Oct. 1959	F51	0	F52, M51	0	m52 ^f , m53 ^f	0	5
Jan. 1960	F51	F52	M51	0	m52	0	4
BAND 6 ^a							
Dec. 1959	F61, F62	0	0	0	m61 ^h , m62 ^h	0	4

^a Mother was either F10 or F11.

^b M11, M12, and M13, all subadult male members of Band 1 in 1958, had become solitary adults by July, 1959.

^c Mother of f35 and f36 was F31.

^d Mother of f37 and m32 was F32.

^e Mother of f45, f46, and m41 was F41.

^f Mother of m52 and m53 was F51.

^g This entire band was live-trapped in December, 1959, and kept in captivity from then on. The two juveniles died in January, 1960. Both females had litters in April. F62 and her entire litter (2 females, 2 males) died in May. F61 and two of her juvenile females were released in June; her remaining juvenile female was retained as a captive.

^h Mother of m61 and m62 was F61.

Bands with 20 to 40 members have frequently been reported in the literature; and although even experienced observers may well overestimate the size of coatis bands, which usually explode in all directions when startled, they undoubtedly reach this general size range under the proper conditions. Reports of "bands" with 200 or more members (Alvarez del Toro, 1952) are probably based on sightings of large temporary aggregations at a particularly good food source. Such aggregations, composed of a number of bands and solitary males, were seen several times on Barro Colorado in the course of this study.

The bands I watched were not very stable. Subgroups frequently left the bands voluntarily and remained apart for periods of up to 2 or 3 days, though usually for less than 24 hours. The subgroups might split again, some of them rejoining another subgroup, so that a diagram of the splittings and regroupings would at times resemble a loosely braided cord. Although any coati in a band might go off by itself for awhile, and a given subgroup might have any composition, the splitting was not random. Certain members of the band tended to stay together, whereas others were more independent and frequently left for short periods. The most stable subgroup seemed to be the basic family unit of an adult female with her young of the current year. Adult females without young were generally the most independent members of bands. Juveniles were seen on several occasions apart from the rest of the band, but I think these were accidental rather than voluntary separations.

Band 1 was the least stable of those that I followed. The most stable subgroup in it was composed of F11, F14, f18, f19, and M12; M13 and especially M11, F12, and F13 were more independent. F15, F16, and F17 were split off from the main group most of the time I was following Band 1, perhaps partly owing to my presence, for they were very shy of me. However, in February, 1959, they began moving into the band again, and by the end of March they were fully integrated.

Band 3 was smaller and more stable. F32 was the only independent one, and was recorded apart from the band 12 times. Her young, m32 and f37, were both with her on 6 of those occasions, each was with her without the other once, and 4 times she was alone. After the deaths of F31 and F32, the stability of the rest of the band decreased. F33 and m32 soon disappeared permanently, and f36 followed not long after that. The remaining small group of F34, f35, and M31 was quite stable.

There was evidence that Band 5 split into subgroups before I had any direct contact with it, and the group I tamed (F51, F52, M51, m52, m53) was joined from time to time by 2 other full-grown coatis that had been seen with the band earlier.

Band 4 was relatively stable, but infrequently F42, F43, and F44 left, either alone or together, for periods of less than 24 hours.

Often no effort is made to keep the bands together—a subgroup casually walks off and neither it nor the rest of the band make any immediate effort to reunite. An adult female may even leave her young behind if they do not see her leave and follow. The deserted young usually remain with the rest of the band until their mother rejoins them, but they often do not maintain as close contact as do the

juveniles whose mothers are present. Three times F32's young became separated from the band and spent 1 to 5 days by themselves before they managed to rejoin the band.

At other times single coatis or groups are clearly uneasy when they become separated from the rest of the band by accident, or because of the voluntary departure of another group. This is especially true of juveniles and single subadults or small groups of them, but it is sometimes true even of adult females with their young. Accidental splits in a band often occur when one group remains to rest or feed in a particular tree or brush pile, while the other moves on, feeding in the litter. Before long, the coatis that were left behind chitter and run to catch up, or the group ahead may wait or turn back, chattering, to find the others. If the members of a subgroup are not immediately successful in finding the rest of the band, they run in looping search patterns (described on page 114) until contact is reestablished.

In general, I do not believe that the splitting of bands into subgroups had anything to do with my presence. One possible exception was the unusual independence of F15, F16, and F17 during the early months of my contact with Band 1. In the light of other evidence, however, even this was probably only the intensification of a tendency that already existed. Subgroups were definitely identified from Bands 1, 3, 4, and 5 before I began taming any of them. After the bands were tamed they were often split into subgroups when I made contact after an absence of several days. While I was following one such subgroup, other members of the band often joined it, showing no signs of alarm at my presence. Or if I was following an individual (e.g., F11 or F32), it often rejoined the rest of the band. The coatis that left the bands while I was following them were often the tamest ones, and when such splits occurred I could easily follow whichever group or individual I chose. In the course of a single day I might be with an entire band, then one subgroup, the entire band again, then a different subgroup, and so on.

SOLITARY MALES

Males usually leave the bands at the end of their second year, at approximately the time when their testes descend. From then on they lead solitary lives except during the mating period, when they may join a band temporarily.

I learned to recognize eight solitary adult males that were frequently seen during the course of this study. MSa was usually seen in the core area of Band 1, but spent much time in the core area of Band 3 while the hogplums were in fruit; he had contact with both bands. MSb was seen chiefly around the laboratory clearing, but also wandered at least 900 meters from it. MSc and MSh were seen only around the clearing, but frequently were absent and also undoubtedly wandered over a much larger area. MSd was seen both around the laboratory clearing and in the home range of Band 1, which he joined during the unsuccessful 1959 mating period. MSe was seen in Band 5's home range. MSf and MSg were both seen in Band 4's home range, and MSf joined Band 4 during the 1960 mating period. All of these males were three or more years old except MSg and MSh, which were both in their third year. Several other solitary males were seen from time to time within the study area, but these were not individually identified.

A single solitary female (FSa) was observed in the vicinity of the laboratory clearing in 1958. She had been observed around the clearing for some months before my arrival in July, and was still ignored or treated with hostility by all of the adult males and by Band 1 when I captured her in September. She died in captivity in June, 1959, and her worn-down teeth indicated old age.

A recently adult male (in his third year) was seen with a female several times in September, 1959, in what had been the core area of Band 3. These two were probably the remnant of a band (possibly M31 and F34 from Band 3); the male had so far failed to become solitary. This was the only adult male I saw regularly associated with an adult female outside of the mating period.

TABLE 4
AGE AND SEX DISTRIBUTION OF KNOWN COATIS IN STUDY AREA
(Nonbreeding Season)

Band	Males			Females		
	Adults	Subadults	Juveniles	Adults	Subadults	Juveniles
1.....	..	3	..	4	4	2
3.....	..	1	1	2	2	3
4.....	1 ^a	3	1	2 ^a
5.....	..	1	2	1	1	..
6.....	2 ^b	2 ^b
Solitary.....	12+	1
Subtotals.....	12+	5	6	13	8	7
Totals.....	23+			28		

^a Does not include 1960 litters (sex not determined).

^b Does not include 1960 litters (5 females, 2 males).

AGE AND SEX DISTRIBUTIONS

The age and sex distributions of all coaties positively identified in the study area are summarized in table 4. The count of solitary males is very probably lower than the actual number present—these males are usually inconspicuous—and the sex ratio for the entire population is probably about 1 : 1. Of more significance in population dynamics, however, is the ratio of adult males to adult females during the mating period. There are definitely more adult females in the population at this time, for females in their second year may breed while males of the same age are immature. But there is still a surplus of adult males, since only one male joins each band in the mating period, and may mate with all of the females in it.

PATTERNS OF SOCIAL BEHAVIOR

All the basic social behavior patterns are listed first, with a very brief description of each. The relevant behavioral context is discussed next, followed by an integrated interpretation of these patterns, which will serve as a basis for the discussion of social relations and the possible advantages to the coaties of these behavior

patterns. I have followed the usage of Moynihan (1955a, b) for such behavioral terms as "motivation," "drive," "ritualized," "hostile," "appeasement," and "re-directed."

COMMUNICATION PATTERNS

Vocal communication.—Coatis respond to different situations with a variety of vocal patterns, which in turn elicit fairly predictable behavior from other coatis. These basic vocal patterns could be subdivided endlessly according to small morphological differences. But unless they can be recorded on tape for analysis and comparison, nothing is to be gained by splitting continua of intensity into multitudes of discrete, named signals when the contexts of the different signals and the responses to them cannot be defined and correlated with equal precision. Because I had no equipment for recording sound in the field, and because the behavioral contexts of vocal signals in wild bands are so complex, I am limiting this presentation to patterns which are easily distinguishable on the basis of accompanying behavior and events.

1) Grunting. Short, throaty sounds of low frequency, usually uttered in series. Low intensity grunts are made by all members of a band while traveling and feeding on the ground. These grunts are made at a rate varying usually from 3 to 6 per minute (based on counts totaling 611 minutes), with extremes of 0 to 10, or more. Grunts range in an apparently complete continuum from this relatively slow, low volume series to the loud, rapid bursts of grunting used in situations of acute alarm. The sound seems to be basically the same throughout this continuum but progressively increases in volume, sharpness, and rapidity of emission.

2) Barking. Single, short, loud grunts. The bark is uttered when a coati makes a reflex jump away from some previously unnoticed object that has suddenly alarmed it. Juveniles often use a high-pitched squeak in similar situations.

3) Whining. Very high-pitched, thin cries, made with the mouth closed, and audible for only a few feet. This sound was made infrequently and only by juveniles.

4) Chittering. A rapid series of short, high-pitched, birdlike sounds. Chittering is most characteristic of very young coatis, and becomes progressively less frequent with advancing age. Although chittering is usually loud and shrill, juveniles make a quieter, more musical chittering in mutual grooming situations.

5) Squealing. Piercing, high-pitched cries. Chittering grades at very high intensities into an unbroken squeal. Frequently the squeal given by adult females is lower in pitch and more nasal than the common squeal, but the high-pitched squeal is used in actual fights.

6) Growling, snarling. Low-pitched, throaty growls and snarls (high intensity growls) are commonly uttered by adult males in the same situations in which squeals are used.

7) Chop-chop. A purely mechanical sound made by opening and closing the mouth rapidly ("biting air") 2 or 3 times in rapid succession. The visual component of this signal may be as important as the sound. This pattern was performed chiefly by adult males, and it was observed only in the breeding season.

8) Chuckling. A complex, frenzied sound with both high- and low-pitched components. Chuckling was heard from coatis of all ages, but most often from adults and least often from juveniles. Ninety per cent of the 50 observed instances were in the breeding season, all but 2 of the others were in December, and 1 of those occurred in a short period of apparently low level sexual activity in late September-early October, 1958.

Visual communication.—Coatis have very few postures that seem consistent and ritualized enough to function as signals. Those which seem most likely to serve as such are listed here, but the evidence for some is weak.

1) Nose-up. The only essential component of this posture is the up-turned snout, and this is all that was observed in some low intensity situations. Usually, however, the mouth is open, the lips

are drawn back exposing the teeth, and the ears are laid back. Other details of the posture depend on specific details of the individual encounters. Coatis defending food from other coatis usually sit or crouch over it. If no food is involved they may either sit or stand, but in high intensity situations and at close quarters standing with the tail out behind, usually at or below the horizontal, is the rule (fig. 7, *a*). The neck may be extended or withdrawn, depending on whether the animal is on the offensive or the defensive. In general, the attack position is head up, neck extended, rump up, and tail straight out behind; the defense position is head up, neck withdrawn, rump and tail down.

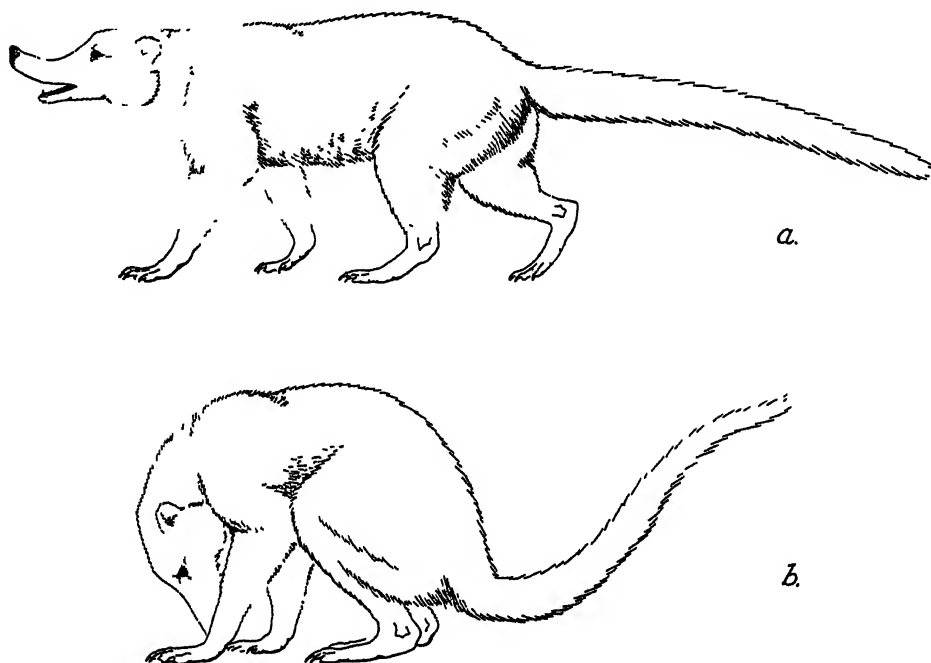


Fig. 7. *a*. Typical high intensity nose-up posture. *b*. Typical high intensity head-down posture. Drawn by Gene M. Christman from photographs by the author.

2) Head-down. In this posture the head is pointed down at the ground (fig. 7, *b*), and in extreme cases juveniles (and rarely older coatis) cross their front paws over their snout or eyes. This posture can be assumed in either a sitting or standing position. The eyes are often partly closed, the lips are never pulled back, and the mouth is usually closed; occasionally coatis make chop-chop sounds, grunts, or low growls while in this position, but for the most part they are silent. The neck is never extended, and the tail is usually not raised.

3) Yawning. Occasionally coatis in the head-down position yawn conspicuously. They frequently look away while yawning, and often partly close their eyes.

4) Juvenile head-jerking, inhibited biting. Juveniles frequently approach adult females (particularly their mothers) when the latter are grooming themselves or other coatis and, lying in front of them, jerk their heads toward the females, make inhibited biting movements at them, and chitter softly. The females usually respond by grooming the young. Especially during the breeding season, inhibited biting frequently is combined with mutual grooming by subadults and adults of both sexes.

5) Tail-switching. Switching the tail jerkily from side to side.

6) Tail-to. In the mating period adult males accompanying bands often approach adult females and sit or lie near them with their tails toward them. Adult females sometimes assume this same position after approaching adult males. The tail itself is not oriented in any particular way.

7) Other positions of the tail. During stop-watch observations in the field totaling 465 minutes, tails were held more or less erect (45° or more above the horizontal) about 40 per cent of the time. The tails were raised and lowered independently of whether the coatis were feeding in the litter, digging, running, or walking. Alarmed coatis frequently raised their tails, but if they were already raised they were often lowered. In encounters with other coatis the tail may be held in any position, though it is usually not held vertically in high intensity nose-up postures.

Olfactory communication.—Olfactory signals are undoubtedly far more important to coatis than can be determined by field observations, especially for species and individual recognition and for indicating breeding condition. Two obvious behavioral patterns connected with olfactory communication were observed.

1) Urine-rubbing. Urine is rubbed on trees, logs, and vines by adult males in the breeding season. They emit the urine while they rub their abdomens up and down on the stems (or forward and back on horizontal logs) by alternately extending and flexing the hind legs; the front legs are used to steady the body (pl. 11). Any trunks and vines more than 2 or 3 inches in diameter may be used.

2) Perineal sniffing. During the breeding season I occasionally saw coatis sniffing at the perineal regions of other coatis.

BEHAVIORAL CONTEXT OF COMMUNICATION PATTERNS

Vocal communication.—1) Grunting. The low intensity grunts characteristic of bands while feeding or traveling are definitely made oftener by females with young than by other members. But further comparisons of age and sex groups cannot safely be made, since the counts were affected by such factors as my presence (e.g., shy animals increased their rates of grunting when I got close enough to them to make an accurate count). An individual may suspend its grunting while it is ripping open a log, digging a hole, etc. Members that voluntarily leave a band to forage alone grunt less frequently than when they are part of a group, if at all. These changes in the patterns of grunting due to influences other than my presence, plus abundant observations of pattern changes in individuals and bands that had not yet detected my presence, argue against the possibility that low intensity grunting was simply a universal reaction to my presence.

There are many situations in which the volume and rapidity of grunting may increase slightly (or begin if the animals have been quiet). Any of the members of a group may increase their grunting in response to the chittering of a coati separated from the group. This reaction is most noticeable in females with young and least noticeable among subadults, but even adult males respond in this way when they are with a band during the mating period. Coatis that chitter when they are separated from a band move toward the individuals that respond with increased grunting and soon rejoin the band. While they are running to catch up, they themselves may grunt slightly more loudly and frequently than is usual when they are with the group. Juveniles that remain on the ground when their mothers climb a tree to feed on fruit may increase their grunting temporarily, but soon quiet down. The members of a band will also respond to the chittering of coatis in other bands nearby with increased grunting. But this situation is complicated by the fact that grunting usually increases whenever another band is encountered, or even when part of the same band returns after an absence, whether or not there is any chittering. While the band is dispersed and the new young are still in the nests, two

adult females from the same band will begin low intensity grunting if they happen to meet briefly in the course of their otherwise lone and silent foraging trips.

Slight increases in the volume and rapidity of grunting were also noticeable when a leisurely feeding band started traveling more steadily; after dusk, when the band usually bunches up more than is usual in daylight traveling; when lone individuals or members of a band were slightly alarmed by some sound or movement I made or I simply approached too close to shy individuals; and when I fed the coatis in a group.

Louder, more rapid grunting is characteristic of other situations. When a member of an unfamiliar band became aware of my presence on the trails or in a blind, the usual reaction was an immediate outbreak of excited grunting. The members of the band that had not yet detected my presence became alert, moved away from the individual doing the grunting, and frequently dashed a short distance up nearby trees. Tail-switching was often combined with grunting in such situations. If the grunting continued, the whole band then moved off together. Bands that frequented a bait station, but were not yet sufficiently tamed for me to follow, frequently approached the blind cautiously, sniffing constantly, then began grunting and hastily retreated a short distance. Even after most of the members of a band were tame enough to follow, some of the shyer individuals would keep well away from me and begin grunting excitedly whenever I came close to them. Once a band was tamed, this loud, rapid grunting was no longer directed at me, but was still a common reaction in other situations. Turtles and snakes encountered in the field, or placed near coatis in the clearing or in pens, usually elicited excited bursts of grunting, often accompanied by a quick retreat, while nearby coatis hearing the outbreak of grunting frequently dashed up trees. Adult males that I encountered in the forest sometimes gave a short, well-spaced-out series of relatively loud grunts before they retreated.

Frequently, adult males and members of bands both gave relatively loud and rapid grunts when they encountered each other. Such encounters usually ended with the male being chased off by the band, which, noses up, chattered, squealed, and occasionally actually tackled and bit him. Captive adult males also grunted and shied away when approached by captive female coatis, a captive racoon, and a large boa constrictor.

In the breeding season, and especially the mating period, coatis that at other times avoid each other and react with hostility when they do meet come into closer contact more frequently. Such encounters are almost invariably characterized by grunting of varying intensity, often associated with other vocal signals and actions that indicate a conflict of motivation. The most frequent encounters of this type are those between an adult male and the band that he joins for the duration of the mating period. The male is associated with the band almost constantly for about a month, during which period he grooms and copulates with the females and is generally treated without hostility. When such a male has been away from the band temporarily, his return like that of other members of the band throughout the year, usually causes a slight increase in the grunting of the band members. More significantly, when the male or members of the band approach each other very closely (often on a fallen log or up in a tree) there is frequently an outbreak of

grunting from the adult male, and sometimes also from the female(s) and younger male(s). The grunting in these close encounters is often mingled with chuckling. The participants may go past each other without further incident, one may sit or lie with its tail to the other, they may stand facing each other in a head-down posture, the male may be attacked, they may pause to groom each other, or the male may mount and attempt copulation. Several of these acts may be combined in the same encounter.

For example, in the 1960 mating period MSf was resting on a fallen log when F42, F43, and two juveniles climbed onto the log. He began grunting continuously, rapidly but not very loudly, as they groomed each other near him. Then he suddenly got up and mounted F42, and both animals grunted and chuckled. After he released F42, a juvenile went near him, his grunting became faster and louder, and he grabbed and mounted her, still grunting. She struggled and squealed, F43 lunged at him, and he released the juvenile. Three more times F42 approached the male and groomed and/or sniffed at him briefly; each time his grunting became faster and louder and the female moved silently away from him. A juvenile also approached him several times, and again his grunting increased. The juvenile left each time without touching him or making any noise. Another time when MSf was resting on a log, Band 4 climbed onto it to rest, and he got up and approached them, giving a series of fast, low volume grunts. When he reached the advancing band, he lay down with his tail toward them. The band continued on past him, each adult female (except F44) pausing briefly to groom with him as she went by. He made abortive attempts to mount two of these females. Thirty minutes later the band came back past him on their way to the ground, and again each of the adult females (except F44) paused to groom with him. There was chuckling during the mutual grooming, but no grunting.

Adult males that approach bands by which they have not been accepted usually do so with very loud and rapid grunting. They frequently pursue the females up trees and engage in active fights with them if the females resist (as is usually the case).

In the mating period subadult males in the same band frequently engage in homosexual mounting, and grunting is common at such times—often when they simply approach each other on the same log.

Loud, rapid grunting is also characteristic of the initial stages of the encounters between adult males in the breeding season, for example, when an "outsider" male tries to approach a band already accompanied by a male. Squealing and nose-up postures invariably follow, and the intruding male usually retreats voluntarily or else is chased off by the other; actual fighting occurs frequently in these encounters. While MSf was accompanying Band 4, he frequently climbed alone onto logs and trees and gave a series of fast, loud grunts when no other males were in sight.

On several occasions adult females in bands emitted long, excited bursts of grunting during and immediately after the band's ascent into a tree to rest. On each occasion an adult female was missing from the group. The first instance involved Band 1, and occurred as they ascended at night. F11 was absent, having been accidentally live-trapped shortly before and not yet released. The other instances all involved Band 4. As they ascended a tree to rest one afternoon, F41

began grunting and stopped only after all of the band that was present had ascended (the three juveniles lagged behind). F43 was absent at the time, and there was a troupe of white-faced monkeys in nearby trees. F43 came along later, making low intensity grunts like those of a traveling and feeding band. As she approached, there was a loud burst of rapid grunts from the tree above. She climbed a nearby tree to rest and joined the band when they descended and moved on. After the band had reformed with the new young in May, 1960, the adult females grunted in a similar manner three times in daytime and twice in the evening as they and their young ascended trees to rest or sleep. On these occasions F41, her single new offspring, and f45, f46, and m41 were not present.

2) Barking. On one occasion the object eliciting a backwards jump and a bark was myself, when a wild coati fed to within one foot of me before noticing me. On another occasion the alarming object was a deer that had walked up unnoticed behind the coati. After the initial jump the coati may run off, dash up a tree, switch its tail, or simply return to feeding, depending on the nature and duration of the alarm. Other coaties hearing the bark may similarly climb trees, "freeze," run off, or ignore it after a quick glance to determine the cause of the disturbance.

3) Whining. Captive juveniles whined as I approached their pen with food each day. The three wild juveniles in Band 4 were left in a group by themselves when the adult females were in late pregnancy and the band was dispersed. At dusk the first night they made several false starts up trees and vines, gave low intensity grunts, chattered, and whined. Two days after F42's new young were born, these same three juveniles climbed into her nest tree and were attacked and chased back down. They stayed below in a tangle of vines, several times starting back up a short way, and whining constantly. Finally they descended to the ground and left.

4) Chattering. A juvenile will walk over to a female who is grooming herself or another coati and lie in front of her, take her head in its forepaws, jerk its head toward her, give her inhibited bites, and groom her, all the while producing a low intensity chattering and a variety of soft squeaks and whimpering noises. Adult females usually respond by grooming the juvenile, which continues to make these sounds as it is being groomed.

Juveniles react in a variety of other situations with a more emphatic, louder, shriller chattering. Wild young coaties that I treed or caught by hand responded with very high intensity chattering. Other coaties in the band, and particularly the mother, responded by returning quickly to the scene. I carried one of these chattering infants away with me, and several members of the band followed for a few yards but made no attempt to attack me. A chattering juvenile coati with nose turned up frequently may advance toward a solitary male that approaches the band. Unless the male retreats immediately and the chattering stops, the young coati's mother rushes to the attack and drives him off. Young coaties also chatter at adult males when they are encountered away from the protective band, but in such situations the chattering accompanies a rapid retreat rather than an attack or a show of defiance. Young coaties sometimes react similarly to the approach of other bands, and may incite hostile encounters between their own mothers and the newcomers. Chattering is also frequently directed at members of the juvenile's own band; for example, at a subadult male that mounts the juvenile during the breed-

ing season, at any member of the band that tries to take food from the juvenile, at other juveniles with whom it is having "play fights," at the mothers of other juveniles which intervene in such fights, and sometimes at any individual other than its mother which approaches too closely. Juveniles separated from the band immediately start chittering loudly; other coatis in the band respond with increased grunting and, from other juveniles, more chittering. If the "lost" coati does not rejoin the band immediately and continues chittering, the other members, especially the mother, move toward the sound. Sometimes chittering heard in the distance is ignored, but if it is prolonged coatis will usually go to investigate. If the chittering stops they will resume feeding again, and the grunts subside to the normal low intensity. Subgroups may split from bands and quietly go their own way for a while. But at other times the members of one or more such subgroups seem to search actively for the other members of the band and the young in the subgroup chitter until contact is made again. Very young coatis just out of the nest chitter whenever they find themselves out of sight of adults, even if other young are present. Young coatis also chitter sometimes during a rain shower.

Coatis less than three months old chitter very frequently—often for no apparent reason—when they are feeding along with the band. As they get older, other vocal patterns replace chittering in some easily identifiable situations; in other situations, the older animals simply seem less "sensitive" than the young ones. Subadults chitter most frequently when they are separated from the band or from a subgroup. Subadults also chitter in encounters with adult males, in encounters with members of other bands, in disputes over food with members of their own band, and in the rain. Subadult females may chitter when approached by a subadult male from the same band in the breeding season. Then mutual grooming often ensues, and sometimes the males mount the females. Adult females chitter occasionally in the same situations, but they do so much less frequently than do subadults. I have never heard an adult male chitter.

5) Squealing. Any member of a band may squeal at other members of the band (e.g., in a dispute over food), at members of other bands, at adult males, or at other animals (e.g., white-faced monkeys that harass the coati). Adult males squeal when facing other coatis in the nose-up position and when fighting. Squealing coatis always assume the nose-up position except when they are engaged in physical combat; squealing is the most common vocalization used in actual fights by coatis of all ages, and the only one used by juveniles and subadults.

The usual response to squealing and the nose-up posture is more of the same. Snarls, chop-chop sounds, and head-down postures may be included, and occasionally a fight results. Nearby coatis often are attracted by squealing, and join in attempts to take food from other band members, in fights between other band members, and in fights between band members and adult males.

6) Growling, snarling. Growls and snarls may be used alone, or alternately with squealing. However, growling is usually restricted to situations short of actual contact. Subadult males growl occasionally, but younger animals typically use chittering and squealing in situations where adult males growl and snarl. Adult females also growl at times, but use low-pitched squeals more often in comparable situations.

7) Chop-chop. This pattern is most typical of adult males in the presence of other males, and is frequently accompanied by urine-rubbing and the head-down posture. Captive adult males also made chop-chop noises when I approached them closely during the breeding season, and on such occasions the head-down posture was commonly assumed. Captive adult females made this sound, often accompanied by rapid grunting, when someone approached them or their new litters. F41 included chop-chop sounds with tail-switching and rapid grunting in response to the sudden noisy appearance of MSf and F42 in the mating period (the three juveniles were also present, and climbed nearby trees, grunting rapidly). The only occasion on which a juvenile was heard to make chop-chop sounds was when my wife cornered a seven-month-old captive male in the breeding season.

8) Chuckling Chuckling was associated with mutual grooming in about three-fourths of the observed instances, either immediately preceding it, or simultaneously with the grooming. It was heard during excited sessions of mutual grooming between members of the same band: adult females, adult females and subadult females, adult females and subadult males. Juveniles often joined sessions, and may have contributed to the chuckling. A very tame captive juvenile female, raised in isolation from other coatis, frequently made chuckling sounds when she was petted and scratched. Chuckling was heard from adult males and adult females during sessions of mutual grooming in the breeding season, and sometimes from the male during copulation.

Coatis from the same band sometimes made chuckling noises when approaching each other after a temporary absence. For example, F14 once made these sounds as she approached F11 when the latter rejoined the band. But F11 responded with squeals, M13 joined in, and the encounter ended in a fight between F11 and M13. Late in the afternoon on the day after Band 4's new young first were seen on the ground in May, 1960, F42, F43, and F44 were resting in a tree with their offspring when F41, her single new young, and her three young from the previous year came in a group and climbed the same tree. There was an immediate outburst of chuckling, grunting, and growling, and the three juveniles from 1959 came hurriedly down out of the tree. The three soon went back up and there was more grunting and chuckling, but this time there was no growling and the entire band remained together there for the rest of the night. The two groups separated the next morning and three days later F41 and her young again joined the other group. The three older juveniles were again treated with hostility by F42, F43, and F44, but F41 joined them immediately for an exciting session of mutual grooming, accompanied by chuckling.

MSf sometimes made chuckling sounds when he approached the females of Band 4 in the breeding season. Other adult males also made chuckling sounds, usually mixed with grunting, on six occasions when approaching bands that they were not accompanying. Three times they were accepted by the females and groomed with them; three times they were met with squeals and the nose-up posture and driven off. Chuckling was heard once while members of two different bands groomed each other during a meeting in late October. Two females that had had no previous contact with each other were kept in adjacent pens during part of the

breeding season. When they were released in June, they ran to each other and began mutual grooming and chuckling.

Finally, chuckling was heard in several situations which started with squeals and nose-up postures, or fighting. 1) In the mating period, a juvenile squealed at an adult male and the male retreated, chuckling. The juvenile's mother then joined the male and they groomed each other, both chuckling. 2) In December, an adult and a subadult female were fighting, with much loud squealing. Suddenly the squealing turned to chuckling and without any pause the two began grooming each other. 3) Again in December, two juveniles began chittering at a subadult female, and their mother ran to join them. In most such situations the adult female will attack in support of her young, but this time there was a brief period of chuckling as the female arrived, and all four animals separated peacefully. 4) In the mating period, an adult female involved in a chain reaction fight was attacked unexpectedly by a juvenile, and retreated hurriedly, chuckling as she went. 5) Once chuckling was heard in an encounter between two adult solitary males. This occurred during October, and was one of several incidents apparently indicating a small peak of sexual activity. The males rushed at each other, squealing, and faced each other with nose-up postures. Then one made chuckling sounds, both rubbed urine on trees and logs, and they went off in different directions.

Visual communication.—1) Nose-up. This picture is commonly assumed in encounters between coatis, especially encounters between adult males, between adult males and members of bands, between members of different bands, and between members of the same band in disputes over a choice item of food. It is also used in some encounters with other animals, as when white-faced monkeys are harassing coatis in fruit trees. Chittering and/or squealing almost always accompany this posture. Nose-up squealing precedes most fights, and occurs during the periods of actual contact.

2) Head-down. The head-down posture is assumed at times by all coatis in the same types of encounters in which the nose-up posture is used, and often they alternate quickly and repeatedly between the two. Coatis in the head-down position may immediately either attack or be attacked; if attacked they assume a nose-up posture and defend themselves. In the mating period captive adult males frequently assumed this position and often licked their feet, abdomens, and penises in the presence of adult females and other adult males. This posture was also assumed frequently by captive and semitame coatis when they were approached by humans.

3) Tail-switching. This action was performed by coatis facing coatis or other animals that had apparently alarmed them. On two occasions, juveniles who were separated from their band climbed trees at the approach of an adult male and switched their tails. Another time, a white-tailed deer approached a band and a juvenile advanced cautiously toward it, switching its tail. A slight noise behind the coati sent it running off in panic. A few minutes later the deer approached a subadult male from behind, and when the male suddenly became aware of its presence he barked, climbed several feet up a tree, and switched his tail. An adult female alarmed by the sudden noisy approach of two other coatis made chop-chop sounds

and rapid grunts, and switched her tail. Adult males and members of bands sometimes switched their tails and grunted as they retreated from me.

4) Tail-to. The response to this posture was not consistent: sometimes the perineal region was sniffed, sometimes the coati that was approached initiated mutual grooming, and females sometimes attacked males who took this position near them. But just as commonly, the tail-to coati was ignored.

Olfactory communication.—1) Urine-rubbing. Urine-rubbing was practiced by both captive and free coatis, frequently by two males when they met. It was often accompanied by chop-chop sounds, and almost always by squealing and nose-up postures. However, lone adult males and adult males with bands also paused frequently each day to mark trees in this way as they wandered through their ranges. Several times males without bands in the mating period were seen rubbing urine on trees as they approached bands. One such male came sniffing along to a tangle of vines at the base of the access route by which Band 4 and MSf had climbed into the tree tops to rest. He sniffed very carefully around the vines, then rubbed urine on them, and quietly went back the way he had come. Three times in the breeding season, adult males retreated and rubbed urine on trees after females responded to their approaches with nose-up postures and squealing.

2) Perineal sniffing. Captive and free adult males were occasionally seen sniffing at the perineal region of females during the mating period. Also, the subadult males in Band 1 sniffed at the perineal region of F11. Once an adult male and an adult female sniffed at each other, and once a juvenile sniffed at an adult male while he was sniffing at a female during a group grooming session. Most of the sniffing occurred during mutual grooming sessions; twice males sniffed at females just after copulating with them, and once a male sniffed at a female that approached him and stood tail-to. In each case the coatis either continued grooming or separated after such sniffing. None of the copulations I observed were preceded by perineal sniffing.

Perineal sniffing was also observed in two encounters between an adult female and adult males just after Band 4's new young left their nests. F44 approached MSf, he sniffed at her, and there were no signs of hostility. The next day F44 approached another adult male, they sniffed at each other, and again there was no overt hostility.

MUTUAL GROOMING

All coatis engage in mutual grooming throughout their lives, but the details of procedure, frequency, and partners vary with age, sex, and stage of the annual sexual cycle (see table 5). Typically, two coatis quietly sit head-to-tail and begin biting rapidly and gently at each other's back with their incisors (pl. 10). Both progress anteriorly and occasionally end by grooming one another's heads, each sometimes using its forepaws to hold and manipulate the other's head. In most instances, however, grooming is confined to the partner's back and no use is made of the forepaws. Mutual grooming is always done with the teeth and never includes scratching the partner with the forepaws. It may occur anywhere on or above the ground, but coatis seem to prefer such elevated locations as trees, fallen logs, and tangles of lianas. Patches of sunlight are also chosen more often than would be

likely by random choice. Blowdowns combine both features, and are frequently the sites of extended periods of grooming and sunning.

The usual pattern is varied when adult females groom their young. The juveniles tend to sit or lie in front of the female, for the most part either squirming around or resting passively, often with their eyes half-closed. The female often uses her forepaws to hold the young coati still and to manipulate it so that she can get to all

TABLE 5
MUTUAL GROOMING

(Boldface type indicates the group groomed with most often and for the longest time.)

Age and sex group	Age and sex groups groomed with		
	Nonbreeding season	Mating period ^a	Period of late pregnancy
Juveniles.....	Mother Rest of band	Mother Rest of band Adult male	Nonbreeders in band
Subadults.....	Adult females Subadults Juveniles	Adult females Subadults Juveniles Adult males	Nonbreeders in band
Adult females.....	Own young Other young Other adult females Subadults Adult males ^b	Own young Adult male Rest of band
Adult males.....	Adult females ^b Rest of band ^b	Adult females Rest of band

^a All mutual grooming increased greatly in the mating period.

^b Rare; mostly near the start of the breeding season.

parts of its body. A really thorough grooming of one juvenile takes from four to six minutes—much longer than most periods of mutual grooming between two adults or subadults. Chittering (page 121) as well as juvenile head-jerking and inhibited biting (page 122) are used by juveniles to solicit grooming, successfully in about three-fourths of the cases that I observed.

When adult males groom with adult females they tend to hold each other's heads in their forepaws, licking and grooming them, more than is common among members of a band. Adult males, like juveniles, frequently lie passively while the female grooms them. Sometimes an adult female approaches an adult male (or vice versa) and sniffs at various parts of his body, prods him with her snout, licks his face, and places her forepaws on his head or back. She may then groom him (especially if he assumes the head-down position), or they may groom each other; but sometimes the other coati responds with a squeal and a thrust of the up-turned nose, or else walks away.

Often other members of a band, especially juveniles, join two coaties that are grooming each other. In the resulting group grooming sessions, the usual pattern breaks down and each participant grooms whatever part of the nearest coati is most accessible. The different members of a band generally move into and out of such sessions freely, and the composition of the group at the end of a session may be entirely different from that at the beginning. Some group grooming sessions last up to an hour, with the various members wandering in and out between periods of dozing, self-grooming, and, among the juveniles, wrestling.

In the breeding season, chuckling was heard during about 40 per cent of the grooming sessions between band members and between adult males and females. This and the soft chittering and squeaks made by juveniles are the only sounds made by grooming coaties.

The open wounds of band members are licked frequently by other band members during grooming sessions. This keeps them clean and no doubt contributes to the coaties' remarkable powers of recovery from wounds.

MOUNTING

In the 1960 mating period adult males were seen mounting adult females seven times. None of these acts lasted more than three seconds, and I do not know if any of them were successful. MSf was seen mounting F41, F42, and F43; all three, plus F44, became pregnant. I am certain that some, if not most, copulation occurs at night. Throughout the mating period the males commonly sleep in the same trees with the bands, or in adjacent trees. Violent chases, squealing, grunting, and chuckling were heard frequently at night from roost trees near the laboratory clearing during the 1959 mating period, and at such times adult males and members of bands were often seen together. MSf frequently slept with Band 4 during the 1960 mating period; movement, chuckling, and grunting were usually heard after they had ascended in the evening and before they descended in the morning.

MSf mounted both F41 and F43 during a session of mutual grooming and chuckling. None of the other mountings however were preceded by mutual interaction. In these, the male walked over to the female and mounted, holding her shoulder between his jaws and grasping her sides between his forepaws. Twice the male began grunting rapidly before mounting, and continued grunting and chuckling until the female twisted free. The other four times the female was passive, and both she and the male were quiet. MSf also twice mounted juveniles in Band 4, grunting rapidly as they came near him and then seizing them in his forepaws. On both occasions the juvenile struggled and squeaked and an adult female lunged at MSf, nose-up, causing him to release the juvenile.

Mounting by juvenile and subadult males was observed on many occasions, especially during the breeding season.

INHIBITED FIGHTING

Inhibited fighting is common among juveniles and subadults, especially in the breeding season. It is apparently a developmental stage and is described under "Further development of behavior" on page 159.

Adult males and females typically engage in some of the elements of inhibited

fighting during the mating period, and this activity, like mutual grooming, seems to play a significant part in their relationship. It includes batting at the partner's head with the forepaws, inhibited biting at the partner's head, and mutual sparring with the head (mouth open) without using the paws. Sometimes these actions are included in periods of mutual grooming and sometimes not, but rarely do sparring matches between adults last more than three to five seconds. One of the partners (usually the female) may end a sparring match with squeals and a thrust of the up-turned snout, but usually both participants separate with no signs of serious overt hostility. On one occasion an adult male and an adult female "bit" at each other's faces just after copulating, but this was the only time any of these actions were directly associated with an observed copulation.

FIGHTING

Actual physical contact is relatively rare in disputes between coatis. Most of the fights are between solitary males, and between solitary males and members of bands. Intraband fighting is less common and occurs chiefly in disputes over food.

The mildest offensive actions consist merely of a quick flip of a paw or thrust of the head toward the intruder, with little or no squealing. Such mild action is especially characteristic of band members in dealing with juveniles, and of adult females in dealing with the adult males who accompany the bands in the mating period. Most disputes of higher intensity are restricted to nose-up squealing, jockeying for position, and impressive charges that seldom make contact. When an attack is launched in earnest, there are often no preliminaries. The attacked animal may retreat, sparring with the forepaws in an effort to ward off the attacker, or it may try to escape by running or (rarely) climbing a tree. Occasionally two coatis will both hold their ground and fight it out, but most fights occur after an attacker has overtaken or cornered his fleeing opponent. If possible the attacker pulls down his adversary from the side or from behind, claspings his forepaws around the victim's back and biting at the back, head, and neck. Or a similar hold may be secured from the ventral side. Several times these holds were maintained for some seconds while the attacked coati dragged its assailant up to ten yards. The two (or more, if a band is involved) roll over, biting, clawing, snarling, and squealing, until one manages to twist clear of the melee and run off. Most of these bouts last only a few seconds, and the "winner" is usually the one who launched the attack. In most fights neither animal is injured, although adult males do quite a bit of damage to each other in the breeding season. The most common wounds are ripped flanks, torn lips and ears, and injured eyes.

When one or more members of a band are involved in a fight, other members of the band usually join in. The result is either a free-for-all, or a chain reaction fight in which each attacker is in turn attacked by another coati, while the previously attacked coatis leave the fight. In either kind of fight the final combatants are often not the same ones who started it.

INTERPRETATION OF PATTERNS

The description of social behavior patterns is an admittedly artificial device for defining terms and presenting data objectively. In reality, of course, each en-

counter involves a combination of these patterns, and the combinations are fairly consistent in similar situations. (Differences in combinations are presumably due to different degrees of intensity of motivation and to the interactions among conflicting drives.) In order to understand and discuss the specific relations between coatis, the data must be reduced to valid generalizations about the significance of certain well-marked and frequently repeated combinations of behavior patterns. This unavoidably involves a certain amount of subjective interpretation, and statements about the motivation behind almost any act are open to question; but the practical function served by an act is shown by the response that other animals make to it, and these can be observed.

Juveniles chatter in a wide variety of situations, apparently as a rather unspecific expression of distress. Whining is probably a low intensity expression of the same thing. In older coatis also, chattering seems to indicate distress, but it is restricted to fewer situations. In coatis of all ages, chattering functions as a "lost call." Coatis that are accidentally separated from their band react by chattering and are aided in rejoining the band by two general responses other coatis make to distant chattering: they increase the volume and rapidity of their grunting, and if the chattering is prolonged they move toward it. Subadults and juveniles typically chatter in hostile situations, and high intensity chattering grades into unbroken squealing. With adults, chattering in hostile situations is largely replaced by squealing, growling, and snarling.

The nose-up posture is a hostile display indicating predominance of the attack drive. Inhibited biting and sparring probably indicate a low intensity attack drive interacting with the mutual attraction of the sex drive. Very strong redirected biting was observed on one occasion: a captive adult male bit viciously at the branch he was sitting on when I backed him into a corner. The head-down posture is the physical opposite of the nose-up (hiding the weapons instead of displaying them), and seems to indicate a subordination of the attack drive in hostile situations. If this is true, the rapid alteration of nose-up, and head-down postures by both opponents in a hostile encounter indicates alternate dominance of closely balanced attack and escape drives. The head-down posture may function as an "appeasement" display by indicating a tendency *not* to attack, thus lessening the attack drive of the opponent. This would be very difficult to prove, however, because of the rapidity of the shift from nose-up to head-down postures. The problem is further complicated by occasional instances of coatis' attacking from a head-down posture. Yawning probably also indicates a tendency not to attack. In the breeding season chop-chop sounds are also made in hostile situations, sometimes accompanying the head-down posture. They are most typical of encounters which do not produce actual fights. The chop-chop seems to be a sort of "ritualized biting," indicating a conflict between strong attack and escape drives, with the latter slightly stronger.

Urine-rubbing is a specialized type of hostile behavior restricted to adult males in the breeding season, and probably indicates interaction between a high intensity attack drive, a slightly lower intensity escape drive, and the sex drive. Since urine-rubbing is used to produce a persistent olfactory signal, it is usually performed in the absence of other males and no other behavior patterns are associated

with it. However, an adult male in a face-to-face encounter with another male, or even a female, sometimes rubs urine in association with chop-chop sounds and weak attack behavior.

Grunting is common in many situations, and although the motivation behind it is sometimes obscure, it has several apparent functions. The low intensity grunting typical of undisturbed bands as they feed and travel, as well as the slight increase in grunting in response to "lost" chittering, seems to aid the band members in maintaining contact with each other. (The intermittently erect tails may also serve this function.) Grunting in all other situations, including slight increases in the usual low intensity grunting, seems to be a clear indication of alarm. This is implied both by the situations which evoke it and the responses shown by other coatis. The bark—a single explosive grunt—is clearly a high intensity alarm signal. The occasional combination of grunting with attack behavior in hostile encounters and its frequent inclusion in sexual encounters demonstrate the conflicting drives which may operate at the same time in one individual.

Tail-switching is apparently an alarm signal, and may also indicate aggressiveness, for it is used in alarm situations only when the cause of alarm is known and in view. Since alarmed coatis often either jerk their tails up or lower them if they have been erect, it may be that any sudden movement of the tail serves as an alarm indicator. (The normal alternate raising and lowering of the tail is much slower.)

Perineal sniffing may be important in determining when the females are in heat: almost all of the cases I observed involved males sniffing females in the mating period. Although it may also function in individual recognition, it is not much in evidence the rest of the year.

Mutual grooming is a positive social force throughout the year. Although it is confined almost entirely to members of a single band in the nonbreeding season, it is an important part of the mating activity. Chuckling is fairly consistently associated with grooming, and seems to function as an inducement to grooming, or at least as an inhibition to aggressive behavior. Its occasional use in hostile situations among band members outside of the breeding season supports this conclusion. Its chief function is probably in reducing hostility between adult males and females during the mating period. The tail-to position may also be an "invitation" to grooming and/or a form of "appeasement" display. Grooming and chuckling are especially important in the breeding season, because all of the mutual activities engaged in by adult males and females at this time, including mutual grooming and copulation, include patterns indicating low level hostility (e.g., inhibited biting, sparring).

THE NONBREEDING SEASON

From about July until January the relations between coatis on Barro Colorado are relatively unchanging. The members of bands travel and sleep together, frequently engaging in sessions of mutual grooming or in disputes over food. The young-of-the-year, now able to run and climb well and to find all of their own food, fit easily into the daily routine of the band. There are occasional more or less hostile encounters with other bands and with solitary adult males, and these males also have occasional hostile encounters with each other.

RELATIONS BETWEEN BANDS

The observed reactions of different bands to each other were the same throughout the year, and the statements made here are based on data collected in both the breeding and nonbreeding seasons. Twenty daytime encounters were observed, and some degree of hostility was evident in all but four. Of these four, two involved small remnants of the same bands, and may have represented the initial stages of formation of a new band. However, the hostility between bands was usually very minor, and physical contact occurred only on two occasions when I provoked fights by throwing food between the members of Bands 1 and 3.

Some of the encounters occurred at fruit trees. In others, when the paths of two bands crossed during their daily travels, one or both of the bands often altered course slightly in order to approach the other. This was not because they were attracted to me, because it occurred in encounters of my tame bands with bands that were not yet aware of my presence, and/or that had never seen me before and were therefore more likely to avoid me out of fear. As the bands approached each other, they slightly increased the volume and rapidity of their grunting. Then there was usually some show of hostility: a few members of one or both bands would turn up their noses and squeal or chitter briefly at the other band and occasionally make short rushes, without contact. Sometimes they assumed the head-down position briefly. Juveniles several times attacked subadults from other bands, and each time the subadults retreated hurriedly. If there was any hesitation in the retreat the juveniles were always backed up by their mothers. After the initial hostilities the two bands usually went their separate ways, or else mixed briefly with little or no further hostile behavior. When two or more bands were feeding together in or beneath a fruit tree there was seldom more than occasional brief chattering to indicate hostility. Mutual grooming between members of different bands was observed only once. Bands 1 and 3 met on October 24, and F32 was seen grooming with two subadults from Band 1, at least one of which made chuckling noises. Several times members of two or more different bands slept in the same roost tree near the laboratory clearing on the same night, but whether or not they slept in the same part of the tree is not known.

Encounters between bands which occurred in the core area of one of them produced no more hostility than encounters in overlapping marginal areas of the home ranges.

On March 14, 1959, the survivors of Band 3 (F34, f35, M31) were seen traveling with two other subadults and one juvenile as though they were all members of the same band. My approach made the three strangers uneasy, and they soon walked off out of sight. The Band 3 group remained intact until April 11, when again I saw F34 and M31 traveling with two subadults and a juvenile. This time F34 and M31 came to me briefly, but they soon hurried off to catch up with the others. This was my last contact with any of Band 3, and I do not know if the new grouping was permanent. No other evidence was seen indicating any exchange of members between bands.

RELATIONS WITHIN BANDS

For the most part adults and subadults in the same band live amicably together with occasional mutual grooming sessions and brief disputes over food. In the few

hostile encounters I observed, adult females were usually dominant over subadult males and females, but sometimes two subadults joined forces to attack a female that was aggressive toward one of them.

The closest relationship within a band is that between an adult female and her young; the next closest is that between an adult female and the young of other females. Juveniles may be anywhere within the scattered group when the band is feeding or traveling normally, but when it is traveling faster after being alarmed, or to seek cover from rain, or to reach a roost tree after dark, the juveniles tend to stay close to their mothers. Whenever their young become involved in noisy disputes with solitary males, coatis in other bands, or coatis in the same band (including other juveniles), females are almost always quick to take the offensive. Only once did I see a female ignore such a dispute; it was between two juveniles and two subadults in the same band. The only coatis that I ever saw stand up to the squealing, nose-up interference of a mother coming to the defense of her young were other juveniles. Occasionally one of them would stand its ground and squeal back, or even attack the female and bite her. On such occasions the female backed off without retaliation. When no disputes were in progress, however, any female would casually shove a juvenile aside with a forepaw when it got in the way.

When their mother is temporarily absent from the band, juveniles are more or less taken care of by other members of the band. Adult females come to their aid when they chitter or squeal and groom them occasionally, though not so readily as they do their own young. Subadults also groom juveniles at times when their mother is not present. After F32 died, her young were frequently separated from the band, and both were permanently lost or dead within a month. About that same time, however, F31 also died, and her young remained with F34, a subadult. In the absence of any adult females, F34 and M31 at least partially took over the role of "mother," responding to the "lost calls" of the young and grooming them more than is usual for subadults. The juveniles retained their dominance over these subadults even though their mother was no longer around to back them up in disputes.

Juveniles are quite belligerent—chittering, squealing, and attacking other coatis that come near while they are being groomed or are eating, or often for no apparent reason. Only other juveniles seem inclined to resist them with any determination. This social dominance results, presumably, from the very real fear other coatis have of the obstreperous juvenile's mother. Sibling juveniles are less belligerent toward each other and their mothers than toward other members of the band. Siblings stay together much of the time, and although they engage in bouts of wrestling and sparring they seldom have serious disputes. All of the juveniles in a band tend to act together in a socially positive manner, but disputes marked by turned-up noses, squealing, and biting in earnest are more common between the young of different females than among siblings.

Grooming.—Mutual grooming is a characteristic band activity and undoubtedly an important factor in keeping the band together. Group grooming sessions are most common between adult females and their young, next most common among mixed age and sex groups in the band, and apparently least frequent between coatis in the same age group. When their mothers are temporarily absent, juveniles

are groomed by other adult females and by subadults more often than when their mothers are present.

The actual number of grooming sessions varies considerably from band to band. Band 3 did more grooming than any of the others I followed. The adult females groomed their young almost every day, sometimes as often as four times in one day. There were one or two group grooming sessions on many days, but sessions involving all other combinations were much less common.

Cooperation and competition.—In discussions of animal societies—from insects to primates—emphasis is usually placed on the coöperation among the various members of the social group. I found little evidence of this in the coati bands, however, except for mutual grooming sessions. There is minor coöperation in roost tree nest-building and in caring for the new young after the band reunites. But the nests in which the young are born are built by each female independently, and each female primarily takes care of her own litter even after the band reunites. The alarm grunts serve as warnings to nearby coaties, just as do the alarm calls of agoutis and other species, and when one member becomes involved in a dispute with a solitary male, other members of the band usually join in against the intruder. However, they are just as likely to join in fights against each other when there is no common enemy, and wrangles over food sometimes develop into chain-reaction fights and free-for-alls.

There is certainly no intentional coöperation in obtaining food. When such prey as a lizard or mouse is scared up, all who see it join in the chase. An animal fleeing from one coati may be caught by another, but such "coöperation" is purely accidental. The coati that gets the prize defends it vigorously against all other coaties in the band, even a female against her own young. The others, attracted by the sounds of eating and by the chittering and squealing of those already disputing over the food, hurry to the scene and try to take the food from its owner, while the latter tries to keep the rest at bay with nose-up squealing and short rushes, not daring to leave the food undefended long enough for an extensive sortie. Often the owner retreats with the food to gain enough time to eat it, but the others usually follow and snatch what they can. This is particularly rewarding when the prey is partly eaten and various parts are lying around loose. The wrangling continues until everything is eaten. Only once did I see an adult female voluntarily allow one of her young to help eat a land crab, and that was after she had eaten most of it herself. A coati engaged in digging a lizard or tarantula from a burrow is usually hostile to all that approach, interrupting the digging long enough for a quick squeal and a thrust of the up-turned snout. Rarely two or more work on the same excavation, but unless the prey is quickly uncovered all but the most persistent digger are likely to leave.

Leadership and organization.—There is no consistent evidence of leadership within coati bands, nor of any organization beyond the general tendency of juveniles to stay with their mothers. There is no fixed dominance hierarchy. Some members are more aggressive than others in intraband disputes, but no member is immune to attack and defeat by any of the other members except, of course, the juveniles, whose high position depends upon support from their mothers. Even their mothers enjoy no such immunity in their own disputes. By artificial feeding,

I could induce in a band a hierarchy based primarily on their reaction to me: the tamest coatis were dominant over those that were more afraid of me. But with one exception, involving a mother and a six-week-old infant (page 158), I never saw any coati, regardless of age or sex, surrender disputed food which was already in its possession to another coati.

There is no obvious leader in the band's daily wandering. When a scattered band is feeding through the forest, the members may be in any arrangement, and the arrangement is constantly changing. Juveniles are seldom in the vanguard, but any of the adults or subadults may be. The adult females are frequently toward the rear while the subadults range on ahead or out to the sides. When any part of a band changes direction, the rest may follow, or they may continue in the original direction, leaving the others to catch up. My data do not show that any individuals or groups (e.g., adult females) habitually exerted even a passive leadership by choosing their own route and leaving it up to the other members of the band to maintain contact. Although any individual or subgroup might leave the band with complete unconcern, any individual or subgroup might on other occasions become disturbed and make an effort to catch up, or turn back to find the others. In general, the fewer coatis in a subgroup, the more likely it was that they would seek to rejoin the rest of the band.

The choice of roost trees at night was not consistently made by any one member of a band; any adult female or subadult might be the first to ascend at night, or the first to descend in the morning.

Leadership, if it exists, should show itself in times of crisis, but although adult females are definitely the chief defenders of their young, I could not demonstrate any such relationship between them and other members of the band. They do not place themselves between a presumed source of danger (e.g., a human) and the rest of the band; neither do the other band members gather around them when danger threatens. There are no "sentinels" posted while the band feeds or rests. Adult females with young are more responsive than are other band members to "lost calls" and make more low intensity grunts while the band is feeding or traveling, but these are presumably part of their immediate role of mother, and probably also function in helping the rest of the band to maintain contact.

In the absence of altruism or coöperation, "leadership" could only be expressed in a general tendency of the band to follow the lead of a particular individual. Whenever there is a difference of opinion within the band in the course of their daily activities, any of three things may happen, based on the relative strengths at that particular time of each member's independent motivation and gregarious tendency:

- 1) If the conflicting independent motivations of the dissenters are not stronger than their gregarious tendencies, the "majority opinion" prevails.

- 2) If the independent motivation of at least one dissenter is stronger at that particular time than its gregarious tendency, and the gregarious tendency is stronger in the rest of the band, the "minority opinion" prevails.

- 3) If the conflicting independent motivations of two or more individuals are stronger than their gregarious tendencies, the band separates into subgroups.

There may, of course, be complications—for example, the tendency of juveniles

always to follow their mother's lead. This, in effect, gives the females with young more influence in the first situation. But true "leadership" would require the consistent success of one individual or small group in influencing the action of the band through the mechanism described in the second. No one individual or group consistently displayed such strong independent motivation. In the absence of further evidence we must conclude that coati bands are only loose assemblages of gregarious animals, usually closely related to each other, and each acting largely in its own interest.

RELATIONS BETWEEN SOLITARY MALES

Mutual hostility was characteristic of all the encounters I observed between solitary adult males; about thirty-five of these occurred in the nonbreeding season and twenty in the breeding season. They are often much more complex than the hostile encounters between adult males and bands, or those within bands. One may include all of the following procedures, though usually some are lacking. Two adult males approach each other, usually near a good food source, and may be as little as ten feet apart before they apparently become aware of one another's presence. Then both "freeze" briefly and stand or sit silently, watching each other. They may assume the head-down posture, yawn, and/or look away, but each remains alert to any move from the other. At this point one may begin nose-up squealing, and the other may do likewise or continue silent, head down. Then one starts walking very slowly toward the other or circles around him. He may pause after each slow step, looking down or off to one side, or sniffing in the litter as if feeding. The second coati may begin circling, too, but usually he starts slowly backing away. Even so the distance between them continues to narrow. Both are silent, and all movements are made with exaggerated slowness. Then the advancing male may quicken his walk and charge, or else charge from a standing position with no advance sign. He may remain silent, or begin snarling and squealing. The "attacked" coati usually backs off hurriedly and may go into a nose-up posture. If he holds his ground the charge usually stops short of contact. The two may then face each other, alternating nose-up squealing with head-down postures, looking away, and yawning. Even if the charging coati reaches his opponent he may go on by if the latter sidesteps, or even swerve aside himself, presenting his shoulder as he lumbers by. The encounter may then revert to more nose-up squealing, growling, and both coatis may begin a series of short rushes and retreats. The coati being forced back may retreat in a squatting position with a series of short backward jumps in which all four feet may leave the ground. If the "attacked" coati does not show any sign of retreating, the other may go on the defensive, back off, and even run away without being chased. Many encounters end when one coati walks off after a short period of squealing. However, if the coati that is charged turns his back and runs, a heavy-footed chase ensues. About a third of the encounters I observed during the nonbreeding season included chases. The chase may end the encounter, or a fight may follow if the pursued is overhauled; however, none of the encounters in the nonbreeding season resulted in fights except when I interfered by throwing food between two hostile males. On the other hand, the pursued may stop, make a stand, and then take the offensive. Back they go in the direction from which they came,

with the roles of pursuer and pursued reversed. This may occur several times, with the direction of the chase changing each time the roles are reversed.

Most of the encounters are less complex than the one I have described, and many consist merely of some nose-up squealing, especially when the males are familiar with each other from frequent contact around favorite fruit trees or in the laboratory clearing. There the three or four most regular visitors developed a fairly well-defined dominance hierarchy. Disputes were brief and the winners could easily be predicted. New males were always subordinate to the regular habitués, but among the latter the dominance relationships changed from time to time. Around food stations, too, the most regular visitors were almost always dominant over newcomers.

On October 3, 1959, MSa and another adult male had what started as a typical encounter, with some initial slow circling followed by short rushes, squeals, and nose-up postures. Then, however, both proceeded to rub urine on logs and trees, and MSa made chuckling sounds. This encounter, as well as the two between MSa and F32 a few days earlier (see page 142), apparently indicated a brief peak of low level sexual activity.

RELATIONS BETWEEN MALES AND BANDS

Of the 63 encounters observed between adult males and bands in the nonbreeding season, about 55 were marked by active hostile behavior, 10 of these by actual fights. Five times the male retreated voluntarily before the band came close, and 3 times adult males and bands fed near each other with no signs of hostility. In over 80 per cent of the hostile encounters, the members of the band were clearly the aggressors. In 5 of the 6 encounters in which the adult male was the aggressor, his opponent was a single coati (usually an immature male) separated from its band. In 3 other encounters between adult males and single members of bands, both coatis were equally aggressive. Most of the encounters occurred at food stations or trees in fruit, but occasionally males approached bands for no apparent reason other than a gregarious tendency.

When a band approaches, an adult male may leave the scene entirely, or else retreat a short distance and loiter on the edge of the group. If he approaches to feed, it is usually slowly and often indirectly. When he gets close some of the band members usually rush at him, nose-up and squealing. Adult females are usually the most aggressive, but they are immediately joined in the attack by the subadults and young. The male may be pulled down by the group in a squealing, biting brawl, and then driven off. Usually, however, the band members chase him only a few yards, break off the attack short of contact, and return to the food. The male remains nearby, and often tries to approach again. He may be chased repeatedly, but frequently he is more or less tolerated after a while and only occasional short rushes and nose-up squealing are directed at him. If the male takes a stand against the band, he and the band members may stand or sit silently, heads down, or alternate this with nose-up squealing. The usual outcome of such stalemates is an unhurried retreat by the male. After repeated contact with a band at a food station or fruit tree, the males often became bolder and less easily chased off. They then fed near the band with little interference. One such male even joined in a free-for-

all among the band members, but they immediately joined forces to drive him off.

A male almost always retreats before the attack of an adult female, even when she attacks alone. When the rest of the band is present, subadults are usually able to force a male to retreat. However, he makes a stand before going far, and often takes the initiative from them if only one or two subadults are facing him and no adult female joins in the encounter. He never presses his advantage, but he is able to keep his harassers at bay. The subadults, too, usually fail to press their collective advantage. Two or more frequently join to drive a male back, but often all but one will turn away and leave the one to face the male alone. One subadult female that suddenly found herself alone facing an unintimidated male immediately lowered her head and began sniffing in the litter as though searching for food, but apparently ate nothing and retreated a few seconds later. When an adult male meets a subadult away from the rest of the band, he usually is the aggressor and chases the other off a short distance, but he seldom presses the attack.

A juvenile coati with a band advances on an adult male fearlessly—nose up and chittering. The male always retreats, and with good reason. If he turns and runs nothing further is likely to happen. But if he only backs off slowly, and the juvenile continues to chitter, its mother rushes to attack. Twice when I was with juveniles that were separated from the band, however, they reacted to the approach of an adult male by dashing up a nearby tree in evident alarm. Both times the males ignored the young coatis completely. I also saw an encounter between two juvenile females, a subadult female, and an adult male. Both juveniles stood their ground, squealing at him, but the subadult was much less aggressive and faced him only intermittently. The male did not attack either of the juveniles, but he did charge the subadult once and knock her down.

On September 26, 1958, MSa joined F32 in an excited session of mutual grooming during which the male chuckled. He also lay still while she groomed him, and each licked the other's face. The next day the same two coatis again joined in a session of mutual grooming, but they were joined by several juveniles and subadults and the ensuing scuffle ended with F32 leading an attack on MSa. On two other occasions in the nonbreeding season adult males were seen grooming with band members with which they had had repeated contact, but these were in December and probably indicated the onset of the true breeding season.

In two other incidents, behavior resembling that of the mating period may have indicated an active sex drive in the adult males after the end of the breeding season. In July, 1958, and in June, 1959, adult males were seen aggressively pursuing bands. One of these males was repulsed by the combined stand of several squealing band members, but the other pursued the band through the tree tops until he caught up with them and was driven off in a fight. This behavior was very similar to that seen in the mating period in 1960 when apparently unmated males tried to approach unreceptive bands.

THE BREEDING SEASON

The coatis on Barro Colorado have a single annual breeding season which coincides roughly with the dry season. The mating period in 1959 was poorly defined and, on the whole, not very successful. None of the females I was following bore young,

but other females in advanced pregnancy were seen on the island as late as May 20, and a female with new young at least five weeks old was seen along a trail on June 13. Juveniles were scarce on the island the following year. The 1960 mating period, in contrast, was sharply defined and more successful, and all of the adult females in Bands 4 and 6 gave birth to young within a period of a few days in early April.

The behavior associated with the birth and early care of the young has a profound effect on the organization and activity of the entire band, and the typical relations and routines of the nonbreeding season are not fully reestablished for two or three months after the young are born.

THE MATING PERIOD

The mating period, which lasts about a month, is characterized by distinctive changes in the behavior of adult males and the members of bands, and in their relations with each other. In general, hostility between adult males increases, but decreases between adult males and the members of bands. This is accompanied by an increase in mutual grooming and by the appearance of copulatory behavior in males of all ages. The diagnostic features of the mating period are the actual association of the adult males with the bands and sexual activity. Other behavioral peculiarities of the mating period persist for several months, however.

The dry season of 1959 actually began in mid-December, 1958, and lasted through April. The most conspicuous mating activity was observed from late January to mid-March. But there were probably preliminary indications of the approach of the mating period as early as December 6, when I saw mutual grooming between MSc and F13 in which they nuzzled, chuckled, and held each other's heads in the forepaws. Except for a few such grooming sessions, no further signs were seen until late January. The principal activity of the 1960 mating period began at the start of the dry season in early January and continued for just one month. There were again some advance signs of sexual activity in early December, 1959, when the juvenile males in Band 5 began mounting each other.

The mating periods in 1935, 1936, and 1937, as indicated by the absence of a semitame adult male from the laboratory clearing, were January 29 to February 11, January 27 to February 10, and January 26 to February 18, respectively (Chapman, 1938). Each time the male returned he was wounded.

Relations within bands.—In both the 1959 and 1960 mating periods there were significant changes in the mutual behavior of the members of the bands. Mutual grooming between all age and sex groups greatly increased, and was often accompanied by chuckling. F41 increased her grooming sessions with her young to an average of two per day, and in Band 1 mutual grooming between pairs of subadult males was observed for the first time. Grooming in Band 1 increased most between the subadult males and adult females. These sessions were frequently more frenzied than those between coatis of the same sex, and included frequent chuckling, inhibited biting, and clasping of the partner's head in the forepaws.

Five of the sixteen grooming sessions I observed between subadult males and adult females in Band 1 ended in attempts at mounting. Mounting was also attempted with no preliminaries on several occasions. Although there might be a

few seconds of wrestling, the females usually managed to elude the grasp of the males without difficulty, and often even mounting was not accomplished. Rarely was there any open hostility, and sometimes the females remained passive while the males mounted them. Some of these mountings lasted considerably longer than the three second maximum observed in mountings between adult males and females.

The subadult males also frequently mounted each other, but the mounted males were seldom passive. At times three males were involved in a tandem arrangement. Even f19, the only juvenile in Band 1 at that time, was not immune from the copulation attempts of the subadult males. And although I never saw M31 try to mount F34, he did try several times to mount f35. The juveniles always chattered and struggled free when a male seized them. Mounting by the juvenile males in Band 5 has already been mentioned, and in the course of the mating period m41 frequently mounted his sisters. His attempts were clumsy, and sometimes he simply mounted and held on for a few seconds with no pelvic movements.

Another activity characteristic of the mating period was the frequent inhibited fighting among the subadult males and the juveniles of both sexes. In addition to the inhibited biting and sparring with the head and forepaws, which adult males and females also engaged in, the younger animals chased each other through the litter and up and down trees and lianas, wrestled, and crouched and sprang at each other (pl. 11). This behavior was often associated with mounting by the males. But although juvenile females entered willingly into inhibited fighting and often initiated it themselves, they always struggled free and ran off when a male tried to mount them. Juveniles sometimes tried to initiate this fighting with their mothers in the mating period and after, but the latter, like the adult males, were usually reluctant to join.

The attempts at copulation by the subadult males in Band 1 ended early in April, but m41 continued to mount his sisters occasionally in periods of inhibited fighting. Inhibited fighting within the bands went on long after the mating period was over, although there was a sharp drop in this activity at the end of it. The subadult males and f19 continued their fighting until I lost contact with Band 1 in May, and in June MS11 and MS13 (newly solitary) went to each other and engaged in a brief bout of sparring and wrestling when they chanced to meet while feeding in a fruiting *Cecropia* tree. Inhibited fighting was also seen in June in another part of the island among four subadult males who had not yet left their band. The juveniles in Band 4 were still occasionally engaging in inhibited fighting and mounting when the study was ended in June, 1960.

Relations between solitary males.—In the nonbreeding season, only one-third of the encounters observed between adult males included chases and there were no spontaneous fights; in contrast, two-thirds of the encounters between adult males in the breeding season included chases, and there were a number of spontaneous fights. The increased fighting between adult males in the breeding season is reflected in the number of head and body wounds noted at that time. Chapman (1938) graphically described the serious wounds inflicted on one old male at a time when the island's coati population was apparently higher than in 1958–1960. In both years of my study this increased hostility between adult males began with

the onset of the true mating period and continued for about three months. Savage encounters were observed until the end of April in 1959, and until the end of March in 1960.

In the encounters which resulted in fights, preliminaries were kept to a minimum and were often lacking entirely. One male simply charged another on sight, squealing and snarling. If, as usually happened, the attacked coati ran off, he was pursued and the sounds of the fight could be heard in the distance. These chases were extremely fast and furious—totally unlike the rather lumbering, half-hearted chases of the nonbreeding season—and always ended in violence.

Most of the encounters I saw during the mating period were between MSf and other males that approached Band 4 while he was accompanying it. MSf was a powerfully built, heavy male at least three years old. Most of the intruders were more slender males in their third year. This was their first mating period since reaching maturity, and they apparently had no bands of their own. In every encounter, MSf was dominant over the younger males, usually attacking them on sight and always driving them away from the band. For example, one third-year male attacked the females in Band 4 while MSf was absent. Presumably he wanted to copulate with one of the females, but his actions were extremely aggressive, and they tried to fight him off with squeals and snarls. He had one female treed and was driving her out on the end of a limb when a twig snapped somewhere out of sight on the ground. The attacking male and all of the females immediately fell silent, watching and listening. MSf walked into view; the younger male gave a few grunts of alarm, immediately abandoned his attack, and fled through the treetops with MSf in furious pursuit. Both were silent for the most part, but there were brief flurries of nose-up squealing whenever MSf came close. Soon he cornered his quarry at the end of a slender, drooping branch 40 feet above ground, but seemed reluctant to attack him in such a precarious position. MSf spent several minutes trying to get at the younger male from adjacent trees, then finally started down the branch toward him. When he reached him there was a brief, squealing scuffle, and the younger male plummeted to the ground. The long fall apparently did not hurt him, for he jumped up and ran off as MSf scrambled down the tree after him. Soon the sounds of further fighting could be heard in the distance.

On several other occasions younger males broke off their attacks on females and retreated hastily when MSf started for them. Twice younger males that were quietly approaching the band while MSf was with it sniffed cautiously, and just as quietly turned and went back the way they had come, before he became aware of them. On another occasion MSg had actually joined the band during MSf's absence. He was resting near them when he saw MSf approaching, and immediately got up and disappeared quietly in the opposite direction. MSf walked on past the band in the same direction, and five minutes later one heard loud squeals. Once MSf himself was seen to climb back down a tree after climbing part of the way up toward a different band; another large male had appeared in the tree near the band.

Urine-rubbing is also a conspicuous activity of the adult males during and after the mating period. This action is performed throughout the day, sometimes several times an hour, both by the males with bands and by those without. Besides this apparently random marking, adult males also rub urine in some hostile encounters

with other males and even with adult females. In about one-third of the observed encounters, urine-rubbing was associated with chop-chop sounds. In the encounters between males, both participants often rubbed urine.

Relations between males and bands.—Of Band 3, only one subadult male, one adult female, and one juvenile female remained alive during the 1959 breeding season. They were not joined by an adult male, but their hostility to adult males did apparently decrease during the appropriate period: on February 17 they had a hostile encounter with MSa which matched in intensity the similar encounters during the nonbreeding season, but on March 15 they went out of their way to approach another adult male and engaged in a brief session of sparring and mutual grooming with him.

Bands 1 and 4 were each joined by an adult male during the mating period, but one male was better integrated into his band. Since the difference was correlated with the difference in success of the two mating periods, it is instructive to compare them.

Nocturnal activity began in the trees near the laboratory clearing in late January, 1959, and continued until early April. The sounds of violent movement, chittering, squeals, grunts, and chuckling were heard, and at such times a flashlight beam revealed coaties chasing each other, fighting, and attempting copulation. MSd and Band 1 were seen frequently, as well as other adult males and bands I could not identify. It was clear that the disturbances were caused by adult males approaching and chasing the unreceptive band members. In one such encounter M12's shoulder was slit open. This activity occurred at any hour from dusk until dawn, but was most common just after the bands retired for the night and just before dawn.

Band 1 was followed off and on by MSd from February 25 until mid-March, 1959. In this period he was with them for only a part of most days, and not at all on some. Usually he stayed on the fringes of the band, rubbing urine on trees and logs, and approached closely only when the band rested in blowdowns, etc. He was mostly ignored except when he approached a member of the band and tried to groom, and then he was often met with a squeal and an up-turned nose. He retreated immediately each time, and at no time forced his presence on any of the band members. This was in marked contrast to his behavior at night. The subadult males were less hostile to him than were the females, and several times went to sniff at him or groom with him. Only once did I see him grooming with a female, and never did I see him mount a female. He once tried unsuccessfully to mount a subadult male.

Band 4 was accompanied almost constantly by MSf from January 4 until January 31, 1960. He was with the band every day, and though he frequently went off for short periods he was seldom if ever far away. He rubbed urine frequently on logs, vines, and trees, and unlike MSd, who seldom approached Band 1, MSf mixed freely with Band 4. For the first few days most of his close advances were met with obvious, though mild, hostility. Even this slight hostility soon decreased, but it never faded completely. MSf's attentions were actively repulsed from time to time, and latent hostility was evident in the inhibited biting and sparring that he engaged in with the adult females—even during sessions of mutual grooming. His

full subordination to the females was evident throughout the entire period. A quick toss of the snout in his direction was often enough to make him abandon even an attempt at copulation, and almost never were more than a short lunge and a squeal required to make him retreat without protest. The only exceptions to this rule occurred in disputes over food. The entire band, including MSf, continued to compete for choice morsels in the usual coati manner.

Mutual grooming between MSf and the four adult females of the band was commonplace, though F44 was less willing to join him than were the others. As many as five sessions were observed in a single day, and only once in eighteen days of observation did I fail to see at least one. Many of MSf's grooming sessions with F41 were interrupted by the arrival of her three young, but occasionally he participated in group grooming sessions (pl. 10). In addition, he or the females frequently approached each other, although with no further result than some brief chuckling, sparring, nuzzling, tail-to sitting, and/or perineal sniffing. Attempted copulation was rarely seen: five times with adult females, and twice with juveniles. No attempt lasted more than three seconds, though only twice did the females actively resist. Each time a juvenile was seized it struggled and squealed and was rescued by an adult female. The male's constant fear of the females during close contact was evidenced by the frequency of his grunting during all of the interactions listed above. The juveniles occasionally tried to engage him in sparring bouts, but he was inclined to shut his eyes and back away.

MSf usually accompanied the band into their roost tree at night or slept in a tree nearby. For sixteen nights I witnessed either the evening ascent or the morning descent (usually both). MSf slept in the same tree with Band 4 for at least part of ten nights; he definitely slept in nearby trees on four other nights, and probably slept with them or nearby on the other two nights, when he was in the vicinity but had not yet ascended when it became too dark for me to see. Each night when he joined the band in the roost tree, and each morning before they descended, there was a short period of moving around, chittering, squealing, grunting, and/or chuckling. But the grunting and chuckling predominated, and there was none of the violence typical of the nocturnal encounters near the laboratory in 1959.

From time to time, other, mostly younger males approached Band 4, usually when MSf was not in evidence. They were often very aggressive, rushing at the females with loud, rapid grunts; and the females fought them off amid a din of snarls and squeals. The following encounter was typical: a third-year male rushed at the females in MSf's absence and engaged one of them in a fight. She retreated, sparring with her forepaws, but he pressed after her and forced her, with the other adult females, up a tree. He continued his attack on them, forcing them out on the ends of branches. Each time he seemed to have one of them in an untenable position, another of the females came up behind him and diverted his attention by nipping his rump until the cornered female was able to improve her position. The arrival of MSf brought relief to the females, with the result described on page 145. Similar incidents occurred several times, and each time the females were able to hold off their harasser until he was routed by MSf's arrival. Even males that approached the band more timidly were met with squeals and driven off. The one

exception saw me and stood looking at me, grunting rapidly and switching his tail. The females went toward him without hostility, and I heard chuckling as at least one of them joined him behind a clump of bamboo.

MSf also approached other bands when he met them, and tended to be more aggressive than he was toward Band 4. He was usually treated with hostility. However, his grunting was often mixed with chuckling, and at least one of these bands allowed him to join them for a few seconds.

As the mating period came to a close, MSf stopped accompanying the band and several other younger males tried to join it at various times. MSg was the most persistent of these. None of them were very aggressive, and all were ignored or easily repulsed with squeals and short rushes. MSf still joined the band occasionally for brief periods of up to an hour. He groomed with the adult females, accompanied by chuckling, and seemed more inclined to groom, wrestle, and spar with the juveniles than he had been during the mating period. Similar behavior was observed between an adult male and a juvenile male near the laboratory clearing, each rearing up on his hind legs to box at the other.

All of the coatis seemed to show a decided preference for conducting their sessions of mutual grooming, inhibited fighting, and copulation above the ground on logs and vines, or up in trees.

Attempts to breed coatis in captivity pointed up the danger of drawing conclusions about natural behavior from observations on animals in artificial situations. Most of the captives' behavior can easily be explained on the basis of knowledge gained from the coatis in the field, but taken by itself it gives a confusing and badly distorted picture of the relationship between adult males and females.

An attempt to breed coatis in captivity in 1959 failed when the male (Cma) ignored the female coatis (CFSa, CFb) and repeatedly mounted a subadult male *Procyon cancrivorous*. Cma continued to ignore the females even after the raccoon was removed from the pen. MSb and MSd were then captured and placed with CFSa and CFb, for several days each, but there was only mutual hostility between them.

Band 6 was trapped intact in late December, 1959, and an adult male (CMg) was taken in the same trap on the same day. All of these coatis were kept together in captivity throughout the 1960 mating period, and their behavior was comparable to that of the wild coatis at the same period. There was very little hostility between the captive females and male; they groomed and sparred with each other, and the male copulated successfully with both females.

Two other females (CFa, CFc) and a third-year male (CMh), all strangers to each other, were placed in an adjoining pen. The females were hostile to the male at first, but CFa later followed him around and made repeated attempts to groom with him. The male was completely subordinate to both females, usually sitting head-down whenever one of them approached him. He groomed with CFa occasionally (or, more often, sat passively while she groomed him), but never attempted to mount. CMh also exchanged hostile behavior with CMg in the adjoining pen, and was completely subordinate to him.

Tree nests.—Another type of activity that becomes apparent in the mating period has more significance later in the breeding season: the building of tree nests

to sleep in at night, or for resting in during the day. No nest-building was seen in 1959 until March 26, when I watched M31 and F34 make one for themselves and f35 to sleep in. I saw nests built on four more occasions that year, the last on August 8. All were built by bands except the one MS13 built at about the time he left the band to become solitary. In the 1960 mating period Band 4 slept in nests at least six times, and MSf built his own in a nearby tree on three of these occasions. In addition, the band and MSf made separate nests for daytime resting once. Nests were built by Band 4 members for use at night four more times before the temporary disbanding. The last of these was built entirely by the three juveniles while F42 (the only adult present) continued to feed in a nearby fruit tree. After the band split up in April, these juveniles built another tree nest on the only occasion when I was with them at dusk.

The nests are crude platforms of branches and leaves added to such natural foundations as a dense area of limbs and foliage, a pile of debris, a tangle of vines, or a tree crotch. All of the nests mentioned above were flimsy, less than three feet across, and built well up in the crowns of the trees. The nests made by solitary males were slightly smaller than those made by bands. The method of construction is simple. One or more coatis stand at the chosen site and pull in nearby branches with their teeth, forcing them into place and biting through or breaking off the smaller ones. Sometimes the forepaws are used to pull branches to the mouth, just as in feeding, but only the teeth are used to break them. Live, leafy branches, dead sticks, and large leaves are added to the pile. When all of the suitable branches within reach are used the coatis may break off others a few yards away and carry them to the nest in their jaws. Sometimes a dozen or more branches up to about two feet long may be used, but at other times a natural pile of debris is simply rearranged a bit, and a few new twigs are added. The members of a band may work on two or more nests simultaneously, since the nests are usually too small for more than three or four coatis. Nests may be used more than once, though they are usually worked on briefly each time, and frequently new nests will be built within a few feet of used ones. In any event, most of these nests are too flimsy to last more than a few days.

PERIOD OF LATE PREGNANCY AND BIRTH

Disbanding.—None of the females in Band 1 became pregnant in 1959, and the band remained intact at least until April 17. I lost contact with the band after that, but saw all of them except F11 together on May 10. By mid-May M12 and M13 had both become solitary and were frequently seen around the laboratory clearing, as was M11 (now MS11), which had left the band a month earlier. Small groups of coatis, mostly subadults and juveniles, were seen in other parts of the island in late May and early June. On May 20 I saw a pregnant female with two subadults, one of which was a male. The first new young were seen on June 13. From these observations it was impossible to be certain whether the bands remained intact when the young were born, or even whether Band 1 remained intact in the absence of reproduction. Observations of Band 4 the following year definitely confirmed the statement of Alvarez del Toro (1952) that pregnant females leave the band and return only when the young can run well.

During late February and March of 1960, Band 4 gradually became less stable as the adult females began splitting off by themselves or in groups of two or three for periods of a few hours. The three juveniles remained with their mother (F41) when the band was split. On March 29, F42 and F43 slept together apart from the rest of the band, and on March 30, the three juveniles remained together as a unit, but they and all four females repeatedly joined in various combinations and split apart again, apparently at random. In the course of the day I was with a succession of eleven different subgroups, ranging in size from one to seven coaties. At dusk I was with F42, F43, and the juveniles, and these five slept together that night. F43 left the group the next morning, and I was with F42 and the juveniles for the rest of the day. We saw no other coaties, and these four slept together that night.

On April 1 there was again no pattern to the splittings and joinings of the whole band, and MSf even joined the group at one time. Several incidents gave positive proof of a basic change in the relations of the band members at this time. Twice F41 squealed and rushed at her three young, nose up and teeth bared, when they approached her. The juveniles retreated, but remained nearby. Soon after, F41 and F42 engaged in a session of mutual grooming, but failed to include the juveniles who came and sat beside them. Still later, F41 did groom two of her young, but her up-turned nose and low intensity chittering were evidence of her newly developed hostility to them. Finally, F41 was hostile to one of her young that approached while she was grooming with MSf. F42 reacted in a similar manner when a juvenile approached her.

Early in the afternoon F42 left the group. I followed her, and was with her every day after that until her young were born. That night she worked on a nest in a *Scheelea* palm tree and slept in it alone. The next day (April 2) she was joined briefly by F41 and the three juveniles, later by F44 and the juveniles. Once more F41 was seen acting aggressively toward her young, and F42 twice chased them from her when they came close. By dark F42 was alone again, and returned to her nest in the palm. The juveniles were unable to locate her there, and were still whining, grunting, giving "lost calls," and running about anxiously when I lost contact with them. From April 3 to April 7, F42 was alone most of the time. She had one brief meeting with each of the other females, and three times was joined for several hours by the three juveniles. She slept alone each night, and was alone all day April 8 and 9. Sometime on April 10 her litter was born.

Activity of pregnant females.—F42's daytime activity from the time she left the band on April 1 until her litter was born nine days later is summarized in table 6, and her movements are summarized in figure 8.

The nest-building activity was particularly significant. F42 worked on the nest in the *Scheelea* palm for one-half hour on the evening of April 1, and another half-hour the next morning before descending. Dead leaflets from the palm fronds were pulled in to the base of the crown and bitten off, and she made fourteen trips along a frond to an adjacent tree to get leafy branches. The next night and morning she worked on the same nest, but although she slept there the following night she did not add to it. On April 4 before going to sleep she worked on a nest in a large tree near Miller 3 which had been used before as a rain shelter by the band and probably as a roost tree. The crown of this tree was densely overgrown with vines,

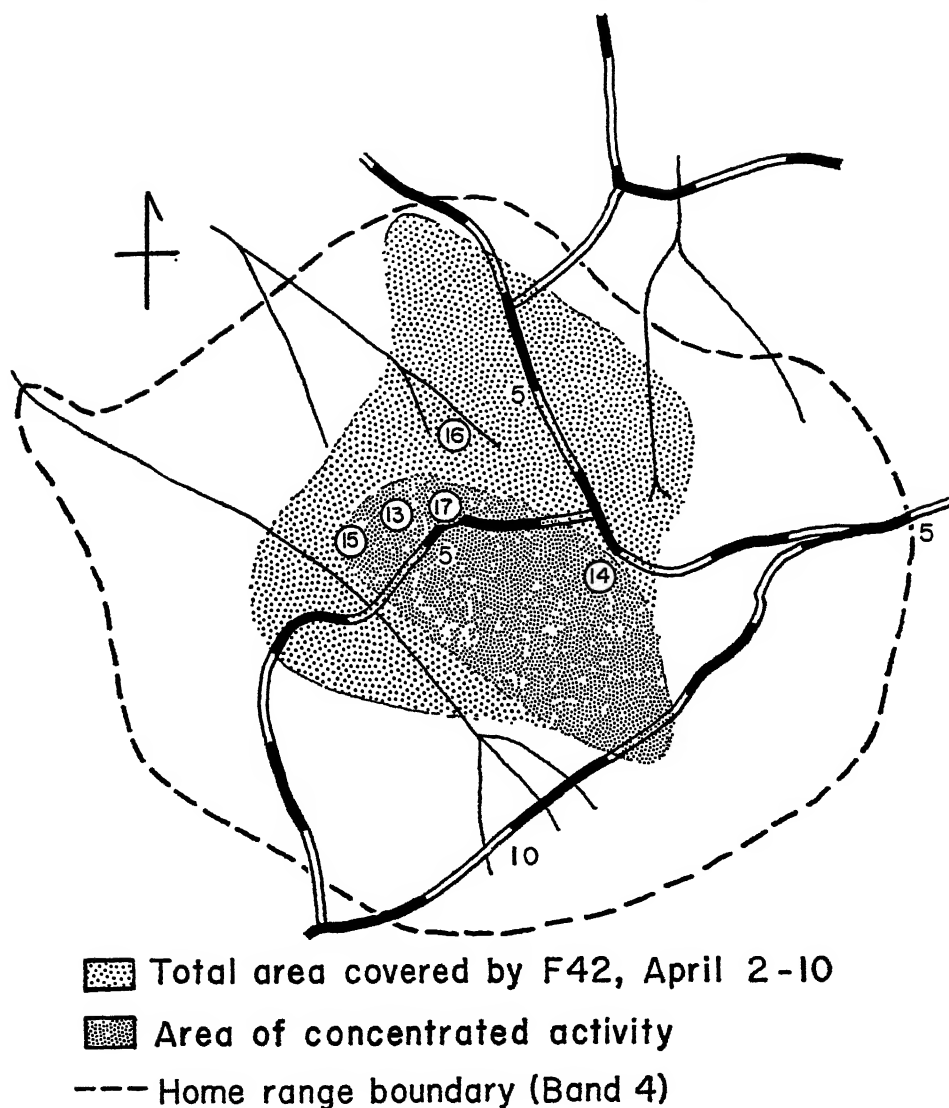


Fig. 8. Activity of F42 in late pregnancy. Trails are marked off in 100-meter sections, which are numbered on the map every 500 meters. The circled numbers refer to roost (nest) trees, which were occupied as follows: 13, F42, April 1, 2, 3, 5; 14, F42, April 4, 6, 8, 9, with new litter, April 10 through May 19; 15, F42, April 6; 16, F41 and litter; 17, F43 and litter.

affording excellent shelter, and it was here that her litter was born six days later. On April 5 there was no nest-building, and she slept once more in the palm tree. On April 6 she worked on four different nests in three different trees. On April 7 and 8 she returned early (before 1600) to the tree near Miller 3 and probably worked on and completed the nest there. On April 9 she explored the tops of three trees and built a small nest in one of them. That night she retired to the nest tree at 1750.

I subsequently located the nest trees of F41 and F43, and all three were within one hundred seventy-five meters of each other (see fig. 8). F43's nest was on a large horizontal limb about seventy-five feet above the ground. It was the only one I was able to see, and was larger (about three feet in diameter) and much more substantial than the rudimentary structures built earlier in the breeding season. F41's nest was in a large almendro tree with a thick growth of lianas.

The meetings between the adult females after April 1—in *Miconia* trees where all the members of the band were feeding—were accidental, and the females ignored each other and soon went their separate ways. MSf was also feeding in one of these trees on April 9 when F42 came to feed, but he made an obvious detour to avoid close contact with her. That evening, however, he ascended the Miller 3 nest tree after F42 had already retired. He may only have been looking for a roost

TABLE 6
DAYLIGHT ACTIVITY OF F42 IN LATE PREGNANCY (APRIL 2-9)

Activity	Hours	Per cent
Feeding and traveling	71.5	67.5
Nest building in trees other than roost trees.....	4 5	4 0
Nest building in roost trees before dark.....	7 0	6 5
Rest	23 0	22 0
Total	106 0	100.0

tree for the night, but if so he picked the wrong one. Within a few seconds after he disappeared into the crown a violent fight broke out, and amid a bedlam of squeals and snarls, down came MSf, half falling, half scrambling, and hotly pursued by F42, who chased him out of sight and then returned to the nest.

The juveniles stayed together throughout this period, changing readily from female to female, and spending much of their time apart from the adults for the first time in their lives. Whenever, they joined F42 they stayed with her for several hours, but there was no grooming, and they always lost contact with her before she returned to her roost tree for the night. The adult was silent on her solitary rambles, and gave low intensity grunts only rarely when the juveniles were with her. They gave both low intensity grunts and "lost calls" freely, but did not maintain very close contact with the female.

Birth.—On the morning of April 10, F42 descended from her nest tree at 0610, fed on the ground, and went back up at 0735. She did not come down again that day, and when I saw her the next morning her litter had been born. I do not know the exact dates on which the other females in the band gave birth, but they must have been close to April 10, because all 4 females brought their young down from the nests within one day 5 weeks later. CF62 and CF61 gave birth to their litters on April 8 and April 11, respectively. These dates are all approximately 70 days from the end of the mating period, which agrees well with the published gestation periods for *Nasua*: 77 days, Canal Zone (Palmer, 1954); 77 days, Philadelphia Zoo (Brown, 1936); 71 days, captive in San Diego (Gander, 1928); approximately 10 weeks, South America (Cabrera and Yepes, 1940).

Coati litters of 3 to 5 frequently have been reported in the literature. CF61 had 3 (all female), and CF62 had 4 (2 males, 2 females). I did not see Band 4's new young until they came to the ground 5 weeks after they were born. At that time F41 had only one, and the other 3 females had a total of 9. (All 9 were together every time I saw them, and I do not know how many belonged to each female.)

EARLY DEVELOPMENT OF THE YOUNG

Because Band 4's new young were in tree nests I was not able to observe their early development and behavior. Such information as I have was gathered from the observations of my wife, Arleen Kaufmann, of the two litters born in captivity to CF61 and CF62 (one of these was abnormal; the young failed to develop properly, and all of the young and their mother died within a few weeks), and from Dr. Ivo Poglayen's observations of a litter born in the Rio Grande Zoo, Albuquerque, New Mexico. Dr. Poglayen has very generously made his notes available to me, and I have combined some of this information with Arleen's in the brief summary which follows.

Color.—The newborn coatis had sparse, dark blackish-gray (Albuquerque) or chocolate brown (Barro Colorado) fur. There were light gray or whitish spots on the head above and below the eyes and at the base of the vibrissae, as in the adult. There was also a variable amount of gray or white on the dorsal surface of the muzzle and on the abdomen, throat, and shoulders. (These areas are also whitish or yellowish in the adults.) The Barro Colorado young had uniformly dark fur on the rest of the body, with no light areas on the ventral regions until a week or more after birth. The light rings on the tail were more conspicuous than they are in the adults, especially on the underside. The original fur was soft and silky, and the long, coarse, yellow-tipped hairs did not appear until the fifth week after birth. The abnormal litter soon lost most of the hair they were born with, and one of them grew a covering of short, kinky, uniformly light gray fur before it died.

Structure.—The weight of the newborn young varied from 100 gm (Albuquerque) to 180 gm (normal litter from Barro Colorado). The head and body length varied from 155 to 165 mm, and the tail length from 100 to 110 mm. At the end of thirty days the weight of the young from both the normal Barro Colorado litter and the Albuquerque litter was 500 gm.

The eyes were closed at birth, as were the external ear openings, and the ears adhered closely to the sides of the head. The eyes of all the coatis in the normal litter from Barro Colorado, plus those of two from the abnormal litter, opened on the fourth to fifth day after birth. However, the eyes of the only surviving infant in the Albuquerque litter did not open until eleven days after birth. The other two coatis in this litter were taken from their mother and died from an unknown sickness. The survivor was left with its mother and apparently developed normally; although smaller than the Barro Colorado coatis at birth, it grew faster and had reached the same weight after thirty days, probably because it was getting the milk produced for the entire litter. All of the other details of its physical development and behavior matched those of the normal litter from Barro Colorado. The auditory canals first started to open six days after birth, and were fully open by the fourteenth day. Compared to the adults, the infants had relatively larger ears and shorter, thicker snouts.

The young were born without teeth. The upper incisors erupted on approximately the fifteenth day, and all of the incisors had erupted by the nineteenth day. The upper canines erupted on the twenty-seventh day, followed a day later by the lower canines. The milk dentition was complete about two months after birth.

Behavior.—The infants made a variety of high-pitched squeaks, but chattering was the most conspicuous vocal pattern and was a common response to being left alone or touched. Whining was also distinguishable in their vocalizations.

The coatís in the normal litter from Barro Colorado were first seen holding their tails erect and walking on the eleventh day after birth. Coördination was poor, however, and four steps was about the limit before they either collapsed with all four legs spread or rolled over. When the latter happened they were able to right themselves immediately. They sniffed constantly at the bare cement floor as they walked, just as adults do when feeding on the ground. Within four more days they were able to walk about two feet before falling over, and had developed a rather clumsy gallop (they tended to push too hard with the hind legs, almost pitching forward on their noses). By the twentieth day they were able to walk with good coördination and now also showed the typical adult feeding behavior of scratching with the forepaws at the ground and at objects such as logs, fallen leaves, etc. Inhibited fighting, mostly wrestling and sparring with the forepaws, was common from the second week on. In a "fight" on the twentieth day we saw a clumsy but recognizable attempt by an infant to mount and grasp another's back and bite at the neck and shoulder—actions used both in fighting and in copulation. Coördination was also poor in scratching attempts, and frequently an infant failed to make contact with its foot, especially on areas difficult to reach. This difficulty was overcome by the end of the second week.

NESTING PERIOD

Band 4's young remained in their tree nests for almost six weeks while their mothers divided their time between caring for the infants and foraging for their own food. F42 spent about half of her daylight hours with her young and the other half foraging on the ground and in trees, seldom more than 200 meters from her nest.

Nursing and grooming.—The females usually sit on their haunches with their forefeet on the ground or a log or tree limb while the young are nursing, twisting around from time to time to scratch themselves or groom the young. This grooming consists mostly of licking, and the teeth are used very little. The female frequently licks the anus of nursing young, which then defecate; the female licks them clean afterwards. In this way the nest boxes of the captives were kept spotlessly clean. The young usually lie flat while drinking, often on their sides. They take hold of the nipple with their forepaws before starting to nurse, and maintain their hold as long as they are drinking. Poglayen reports that very young coatís press alternately with both forefeet as they nurse ("Milchtritt").

Carrying the young.—The females carry their young firmly in their jaws, grasping them around the abdomen, or, more commonly, around the neck. They use their forepaws to roll the infant into position so that it can be picked up more easily. The captive females carried their young in and out of the nest boxes and across the pens away from humans who approached them. One use of the carrying technique in the

wild was dramatically demonstrated by F43 while I was watching her nest. She climbed out and down into the branches below the nest, then lunged, knocking loose some dead twigs, and almost fell. As she struggled to regain her balance, 75 feet above the ground, I saw one of her infants in her jaws and heard it squeaking. She soon had it back in the nest, but one wonders how often the active youngsters get themselves into similar predicaments, especially toward the end of their stay in the nest.

Relations of females with young to other coatis.—In the nesting period when adult females occasionally met, each gave some low intensity grunts and went her silent, solitary way. If one of them met the three juveniles while foraging, again the encounter was brief with no signs of hostility. But around the nest tree, adult females were definitely hostile. On the day after F42's young were born, the three juveniles from the previous year climbed into her nest tree. Within seconds there were violent snarls and a crashing of limbs and vines, and one of the juveniles came plummeting, belly first with legs outstretched, forty feet to the ground. It landed in a patch of small palms on a soft, muddy slope and in a few seconds got up and went to the base of the tree. More sounds of fighting came from above, and F42 chased the second juvenile down through the lianas. The juvenile, half falling, half scrambling, finally lost its balance and fell the last twenty feet, bouncing off several lianas near the ground. Immediately it started back up the lianas into the tree, and went up thirty feet to the place where the third young had been chased by F42. She attacked again, chasing both of them to the ground, but they seemed reluctant to leave, climbing around in the lianas near the ground and whining constantly; they even started up three or four more times. Each time, however, they turned and descended, and F42 remained watching them from about thirty-five feet up. After about five minutes they left.

Four times MSf came by while F42 was foraging on the ground near her nest tree, and each time she chased him out of sight. During most of this action both were silent, but sometimes the female made a series of "squeaks" that sounded like short, cut-off squeals. Once MSf retreated about ten yards on seeing F42 approach (she chased him out of sight anyway), but twice he came back within five minutes, and once he returned her aggressive nose-up display and rubbed urine on a tree.

Social relations of other members of the bands.—I saw one encounter between MSf and the three juveniles. All four immediately began low intensity grunting, and when MSf happened to walk near them the juveniles dashed up a liana a few yards away. He ignored them completely.

My observations of Band 4's three juveniles and of other bands during the late breeding season in 1959 and 1960 indicate to me that the nonbreeding members of the bands remain more or less together in the period when the females with young are absent. However, the subadult males in particular are prone to wander off on their own or in small groups. This increasing independence is a prelude to their complete break with the band within the next few months.

POSTNESTING PERIOD

Reunion of the band.—Band 4's new young left their nests on May 20, 40 days after they were born. Within 24 hours all of the females brought their young down

and reformed into a single band. F42, F43, and F44 combined their litters first; later that same afternoon F41, her single new young, and her 3 young from the previous year rejoined the group. This reunion was not immediately permanent, however. The next morning Band 4 split again into the same two groups, and for the next two days these groups had no contact with one another. On May 24 they met at 1615, but split on their way to the roost trees and slept apart. They were still apart when I saw F42, F43, F44, and their 9 young on May 26; but on May 30 I saw the entire band together: F41, F42, F43, F44, their 10 new young, and f45, f46, and m41, now within a month or two of becoming subadults. I last saw the band on June 4; they were still together, but only 8 of the new young were with them.

The reunions between the adult females were not hostile, but when, on the afternoon of May 20, F42, F43, and F44 were in F42's nest tree and F41 and her 4 young approached and climbed the same tree, there was an immediate outbreak of grunting and chuckling followed by snarls, and the 3 older juveniles came scrambling part-way down. After they went back up, there were more chuckling and low intensity grunting but no more snarls, and the whole band soon settled down together for the night. On May 24, F42, F43, and F44 were resting with their young in two temporary tree nests when the 3 juveniles approached from a nearby tree. The females came part way out of their nests, but without any obvious show of hostility, and the juveniles retreated. Soon the 3 females and their 9 young descended and then the females actively chased the juveniles, which remained nearby. F41 and her one new young then descended from another tree and joined the other females for the first time in four days. All the females joined immediately in an excited session of mutual grooming and chuckling. The 3 older juveniles were again treated with hostility when they tried to join the grooming.

Presumably this is the usual pattern. The females bring their litters down from the nests, reunite, and are joined in the course of several days by the nonbreeders, toward whom they show temporary hostility.

Maturation of males.—The subadult males may remain in the reunited bands briefly before they take up their solitary existence as adults. I have no reason to believe that they are driven off initially by the females with young; it seems more likely that they gradually become more independent and finally sever relations with the band of their own accord. This conclusion is supported by the behavior of M11, M12, and M13 in 1959. All three gradually became more independent through the breeding season and left the band by the middle of May, even though none of the females had bred or showed hostility to these males. Their testes did not descend until July. Other males of the same age were seen with the bands as late as June 20. Late in the afternoon of August 8 I again made contact with the survivors of Band 1: F11, F15, F16, F17, and the now full-grown F19. MS11 joined them, and they amicably went off together. Soon they climbed a roost tree, and the five females worked on two small nests simultaneously, while MS11 remained lower in the tree and did not help. They all settled down to sleep, but at dawn the next morning only MS11 descended. Apparently the females had gone off in the night. Although I searched for them for the next two weeks, I never saw any of the females again. MS11 was seen frequently after that in the same general vicinity.

After the males have become essentially solitary and their testes have descended, they are probably greeted with more hostility by the bands with new young than MS11 was by Band 1. Solitary males do occasionally approach the bands during the nonbreeding season with no sign of hostility. As a rule they are driven off, but two exceptions were observed soon after Band 4's new young descended from their nests. On May 23, MSf was encountered on a foraging trip and F44 ran to meet him. He sniffed her perineal region, and neither seemed hostile. Then F42 joined them silently, turned her nose up at MSf, and he left. The next day another solitary male approached the band, F44 went to him, they sniffed each other, F42 joined them, the male moved off several yards, and the females rejoined the band. Two or three of the new young followed F42 over to within two feet of the adult male and he ignored them completely.

Relations between other members of the bands.—The positive relations of the other members of the band are soon reestablished. The older juveniles in Band 4 were seen briefly nuzzling and grooming the new young, and engaged them in rather one-sided inhibited fights in which the bigger coatis held the little ones fast in their forepaws and rolled them around; m41 apparently tried to mount one. The older juveniles continued inhibited fighting among themselves, chasing each other up and down lianas, sparring, and wrestling. They also tried to initiate such fighting with their mother, and after being pushed around a bit she sometimes joined in.

Behavior and care of the new young.—The new young are well able to climb and run when they leave their nests. They make long unaided climbs into trees several times each day; however, they tend to descend the lianas too fast, pile up behind the slower ones in front, and lose their footing. Falls of up to twenty feet were frequently observed, but the young were always on their feet again and able to climb within a few seconds. Occasionally a female will carry one of her young up a tree in her jaws. The young dig in the litter and in very soft rotten logs and get some food in this way from the time they first leave the nest. They also eat fallen fruit: many black palm nuts were eaten in the few days that I was following the band with its new young. They manage to keep up with the females fairly well on foraging trips, but may lag behind, especially when they are busily engaged in digging just when the females move on or when they cannot negotiate a gully because its sides are too steep or the branch they pick for a bridge does not go all the way across. Since they tend to follow each other, there may soon be a crush of small coatis at the end of the branch, the ones in the lead hard-pressed to avoid being pushed off.

Whenever the young find themselves alone, or out of sight of an adult female, they chitter. The nearest female gives low intensity grunts, and if the young hear they run to catch up. But if they are farther away and continue to chitter the female runs back to them. Usually the female carries off one and the others follow, but sometimes she has to carry several individually to the new location. She may also move each one when she is mildly alarmed and wants to leave but the young, oblivious to the danger, do not follow her. Besides chittering, the new young occasionally give recognizable alarm grunts.

The small young wrestle with each other frequently. They also climb in low bushes and vines, either by themselves or in chases, but far less frequently than older juveniles.

When females pause to groom each other or themselves, the new young run to them, climb all over them, and bite at them in the same manner that older juveniles use to good effect in soliciting grooming. The females are peculiarly unreceptive to such actions from the new young, however, while they are on the ground. In three and one-half days I saw only three abortive moves to groom them in such situations, and these consisted only of brief nuzzlings. Usually the females got up and walked away. In the same period I saw only two or three attempts by young to nurse, and each time the female walked away within a few seconds.

Virtually all of the grooming and nursing of the new young takes place after the ascent into the roost trees in the evening, before the descent in the morning, or in trees during the daytime rest periods. Of 465 coati-hours of daytime observations

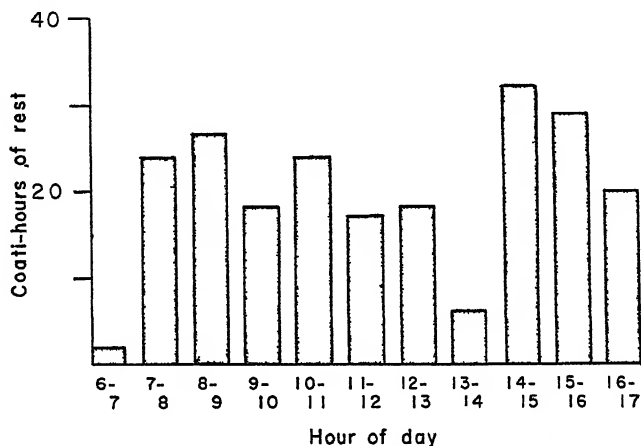


Fig. 9. Hourly distribution of daytime rest periods for Band 4 with 6-week-old young (May 20-25, 1960). Adjustment has been made for differences in the amount of observation in each hourly period.

from May 20 to May 25, Band 4 spent 48 per cent on the ground and 52 per cent in trees resting, grooming, and nursing. There may be two or three extended rest periods each day; the hourly distribution of the daytime rest is shown in figure 9. Nests are sometimes built for these daytime rest periods, and occasionally the band may use the nest in which a litter was born or an old nest in a roost tree. Daytime nest-building was also observed by Dr. C. R. Carpenter (personal communication) while he was studying howler monkeys on Barro Colorado in July, 1959. Dr. Carpenter saw four full-grown coatis, with several small young, building a nest. (One female was seen carrying an infant up to the nest in her jaws.) The young were apparently nursing. When Dr. Carpenter returned thirty minutes later the four full-grown coatis became alarmed, left the nest, and ran off. The young remained in the nest, one in plain sight as it clung motionless to a branch. It maintained this "freezing" position for the full fifteen minutes of observation.

Females are apparently more inclined to share food with the young at this stage than later. F43 was eating a black palm nut when a small juvenile approached and took the nut in its own paws. The female pulled, but the infant held on and the female silently walked away as the young proceeded to finish eating the pulp.

The new litters usually run in a group rather than each following its own mother. Adult females sometimes even go off for short periods, leaving their young with the rest of the band. When a young coati fell from a tree in which the band had been resting, all three of the adult females present ran along the limb, looked down, and F42 went down after it. But the young, unseen by her, started back up a liana on the other side of the trunk and was unable to cross over to the rest of the band. F44 immediately made her way over to it, and escorted it to the ground when the rest of the band descended soon after.

Further development of behavior.—Nursing gradually decreases as the ground feeding technique of the young becomes more efficient. In 1958 I saw juveniles nursing occasionally as late as September 16, at least four months after they were born, even though they were perfectly capable of finding all of their own food.

Although they seldom use them, very young coatis are capable of producing most of the vocal patterns used by adults. The growls and snarls of both sexes and the low-pitched squeals of the females apparently develop only as the coatis approach maturity, but all of the other vocalizations have been heard (some only rarely) fully developed in juveniles. The ability to make chuckling and chop-chop sounds apparently develops later than whining, chittering, squealing, and grunting, which are all well developed in coatis less than two months old. Deciding the exact age at which any vocal pattern develops is difficult, because some patterns may not be evoked (at least in the presence of the observer) until long after they are developed.

Inhibited fighting includes almost all of the observed activities that might be labeled with the much over-used term "play": 1) crouching and springing forward, sideways, and backward; 2) chasing—anywhere, but especially up and down trees and lianas; 3) wrestling, including clasping and biting of the back; 4) sparring with forepaws and head, often combined with rearing up on the hind legs; 5) inhibited biting; 6) covering the eyes with the paws when the "play" gets rough; 7) pulling the pursued down from a tree by his tail, grasped in the forepaws. All of these patterns except the last have been observed in serious fights, but then they are usually performed in a less exaggerated (and less harmless) manner. Most of these actions are performed in silence, though occasionally there is chittering, squealing, or grunting when one of the participants gets too rough. The only "play" pattern that is not a fighting technique is mounting by young males.

Juveniles were observed performing all of these activities in the nonbreeding season, though infrequently. There was an obvious increase in such activities in late November and December, and they were a common and conspicuous feature of the breeding season. Not only the juveniles, but the subadult males as well, participated at this time, and to a lesser degree, so did the adult males and females. The adults responded rather weakly to advances made by younger animals, but sparring and inhibited biting were common between adult males and females. The juveniles persisted in these activities right through the breeding season, even engaging in them with the new young. Both age classes also managed to involve the adult females from time to time. Finally, there was a decrease in these activities as the older juveniles became subadults and the new young reached their second or third month.

ADAPTIVE VALUE OF COATI SOCIAL BEHAVIOR

Communication.—The adaptive value of a behavior pattern, referred to here as its “function,” is independent of any purposiveness in the motivation of the animal performing it. That is to say, the adaptive function of a vocal, visual, or olfactory signal is independent of any intent of the animal sending the signal, or of any conscious “understanding” of the signal by the animal responding to it. In the simplest cases animals evolve automatic responses to a few specific situations, and these responses act as signals that elicit the appropriate automatic responses from other animals. Coatis, however, react to a wide variety of situations, and seem capable of some appraisal of each, based on the available information; moreover, their response to a given signal is modified according to the details of the situation producing it. For example, high intensity alarm grunts may send other coatis dashing up trees if they do not know the cause of the alarm; but if the cause of the grunting coati’s alarm is visible, and the other coatis are not alarmed by it, they may not respond to the signal. Furthermore, the response of an adult female to the chittering of her young depends on the (apparent) cause of the chittering. She may give answering low intensity grunts; or go to investigate; or attack; or, after a quick glance at the young giving the call, ignore the chittering. But this does not imply that the coati giving the signal is trying to convey certain information, which is consciously understood by the receiver of the signal.

The motivation behind a signal may even be unrelated to the adaptive response which has evolved to that signal. For example, although the motivation behind the usual low intensity grunting of a traveling and feeding coati band may be a low level “negative” feeling of alarm or uneasiness—the higher intensities of grunting seem clearly indicative of alarm—the function of this low intensity grunting seems to be “positive,” as a “contact call” helping the band to keep together.

Except for the various intensities of grunting, most of the coatis’ signals function in hostile situations to achieve the adaptive ends of aggression without danger of physical damage. The nose-up posture, chitter, squeal, growl, and chop-chop, all harmless substitutes for fighting, usually decide conflicts without physical violence. The head-down posture may function as an “appeasement” display by intimidated coatis, but the rapid and complex alternation between this and more aggressive displays has made acquiring statistical evidence of its effectiveness so far impossible. It is certain that coatis presenting this display will readily fight if pressed. Chuckling and the tail-to position seem to reduce the hostility of other coatis in social (usually sexual) situations, possibly by inducing the socially positive action of mutual grooming.

I found no evidence that the olfactory “signposts” produced by one male’s urine-rubbing have any effect in driving the other males out of a given area. All the males that inhabit the area continue to patrol it, each leaving his own marks. However, fresh signs may help to minimize the number of hostile encounters between these males by warning subordinate males of the presence of a dominant male in the immediate vicinity. The consistent dominance of some males over others has already been mentioned (e.g., MSf over the younger, unmated males), as has the tendency of the subordinate males to avoid contact with the dominants.

Social organization.—The hostility between solitary males, and the tendency of bands to remain in fairly restricted areas, even without the obvious mechanism of territorial defense, combine to achieve a population distribution which insures efficient use of the habitat and effective reproduction. But the social structure is still flexible enough to allow different units to take advantage of large local food supplies; there is little hostility among the bands and adult males that make up large temporary aggregations feeding on a particular fruit crop.

There are definite advantages in the grouping of females and young in bands—even when they are as loosely organized as coati bands. Coöperation among band members in the face of a common enemy affords increased protection, especially for the juveniles. If a female dies or becomes separated from her litter, the care given her young by the other females and subadults in the band greatly increases their chances for survival. And even though there is no active coöperation in obtaining food, the type of foraging done by coatis is done more effectively by a group. The chance that a particular small vertebrate will be caught is increased when it has to run the gantlet of an entire band. This is particularly true of such animals as the lizards of the genus *Ameiva*, the vertebrates most commonly caught by coatis on Barro Colorado Island, which depend to a large extent on running to escape capture. Each coati benefits from food chased its way by other members of the band, and more such prey is obtained by the coati population as a whole than would be the case if each coati hunted separately.

Mutual grooming not only rids coatis of external parasites and promotes healing of wounds, but also plays an important part in maintaining band structure by providing the members with frequent, socially positive interaction. Inhibited fighting among the juveniles and subadults probably helps preserve band structure by serving as a positive outlet for latent or developing hostility. Inhibited fighting and mounting may also develop skills that are useful in more serious encounters. Low intensity grunting, "lost calls" and the responses to them, and the upright tails all probably aid the members of a band to maintain contact with each other.

Although solitary females are known, there may be some minimum group size (about three or four) below which the members seek to join another band. The occasional association of the remnant of Band 3 with another small group, as well as the tendency of small groups from Bands 1 and 5 to rejoin the bands after they had apparently split off and the readiness with which CFa joined with CF61 and her litter when they were released in June, 1960, is evidence for this. I saw no absolutely certain example of a coati joining a band for the first time. But the behavior of coatis toward members of other bands and solitary males that they meet frequently (as at a food station), the behavior of Band 1 toward F15, F16, and F17 when they sought to rejoin the band, and perhaps even my own success in "joining" coati bands, all indicate that a persistent stranger has a good chance of being accepted. In each of these situations, initial hostility was overcome after constant contact and familiarization, and the "strangers" were eventually tolerated.

Although there may be no maximum size limit on bands short of the limitations imposed by the food supply, the general instability of even small bands argues against the existence of large bands except in a very casual sense.

The most important behavioral change of the breeding season is the association

of an adult male with each band. The male that joins each band is apparently one whose home range overlaps that of the band, and with whom the members are therefore already familiar. Their acceptance of him is presumably due to the combined effect of their previous familiarity with him augmented by his more or less constant presence during the mating period, their decreased hostility toward males in general, and the mutual attraction caused by the activated sex drive. This acceptance of the male is demonstrated most clearly by the frequent sessions of mutual grooming, which in turn strengthen the temporary bond between male and band. The inhibited fighting between males and females and the frequent grunting of males in close contact with band members are constant reminders of the aggressiveness and fear which must be suppressed for successful mating. Sparring and inhibited biting may serve a positive function as a harmless outlet for this suppressed hostility at a time when open hostility would be detrimental to the species. The violent encounters between members of bands and other males during the mating period are further evidence of the importance of the temporary bond between bands and males with which they are familiar.

In light of this, the behavior of captive males and females thrown together for the first time cannot be expected to represent the normal mating behavior of coatis. Our success with CF61 and CF62 was due to our fortunate choice for their mate of an adult male from the same area—possibly the male that would have mated with them if they had not been captured. Males and females kept together for long periods in captivity will sometimes mate, but without field observations we would still be unable to make valid statements about the mating habits of wild coatis.

That one dominant male mates with all or most of the females in a band makes the number of males less important for reproductive success than would be the case if each female mated with a different male. Just as the organization of females with young into bands makes each individual of less critical importance to the survival of the population, so the behavior of the adult males makes each of them of less critical importance to the population. The increased hostility between males during the breeding season coupled with the association of one male with each band also tend to restrict actual breeding to the few strongest males in the area. However, the social structure is loose enough so that gene flow between different segments of the population is not greatly restricted.

With the approach of parturition, the pregnant females undergo another change in behavior—this time toward members of their own band. Each pregnant female leaves the group voluntarily. There is no increased hostility between such females, but they develop a definite hostility to the nonbreeders (including their own young). If these nonbreeders remained with the females, they would pose a threat to the newborn young. The birth and early care of the young in tree nests reduce the chance of their being found by predators, and presumably make them easier to defend than they would be on the ground. The greater safety of the treetops is also indicated by the refusal of the females to groom or nurse their young on the ground for some time after they leave the nest.

INTERSPECIFIC RELATIONS

In general, my observations of interspecific relations show that the coatis and the vertebrates they encounter pay little attention to each other. The scientific names

given here for mammals are those used by Hall and Kelson (1959); the scientific names for birds are from Eisenmann (1952).

PREDATORS

Pumas (*Felis concolor*), ocelots (*Felis pardalis*), and jaguarundis (*Felis yaguarundi*) have all been seen on Barro Colorado, but none (as of January, 1961) since a puma was observed in 1957. All are potential predators on coatis, though they probably concentrate on deer, peccaries, and rodents.

Boas are also potential predators, especially on young coatis. Sanderson (1941) reported finding coati hair in the stomach of a boa constrictor he killed. *Constrictor constrictor* is common on Barro Colorado. Live boas seven and eight feet long were presented to coatis on two different occasions, once to an adult male, and once to Band 1. On both occasions the snake showed no interest in the coatis and started off in the opposite direction. The coatis' reaction was one of mixed alarm, aggressiveness, and curiosity. There was no panic, and several of the coatis approached the snake cautiously when it started away from them. One of the subadult males in Band 1 even crept up and bit it on the tail as it was leaving.

Harpy eagles (*Harpia harpyja*) and several other large birds of prey have been seen on or over the island from time to time, and these are also potential predators on coatis. Mr. Philip Welles showed me a photograph of a coati killed by a golden eagle (*Aquila chrysaetos*) in Arizona.

I never saw any attempt by a predator to kill a coati; however, several juveniles were observed with large open wounds. One of these was one of a pair that was separated from Band 3, and rejoined the band five days later. The other was never seen again. From what I observed of the relations between young coatis and adults, including solitary males, I doubt that these wounds were inflicted by other coatis.

PARASITES

Mutual grooming sessions probably serve partially to control external parasites, and so may the considerable time coatis spend scratching and grooming themselves with their teeth. Occasionally I have seen one or more large ticks hanging on a coati, but these usually fall off in a few days. Ticks are more common on solitary males, especially when the animals have poor pelts and seem emaciated. Ectoparasites are possibly an indicator of poor condition rather than a primary cause.

Bot fly larvae of the family Cuterebridae commonly cause large swellings on the bodies of howler monkeys, and I saw two cases of such parasitism on coatis. One larva caused a swelling like a miniature volcano with a small opening to the outside on the flank of a juvenile. The bot dropped out after about a month, and apparently caused no permanent ill effect. The coati scratched at the swelling frequently, especially as it got larger, but otherwise was not hampered by it. The other case, which involved an adult female, was similar in every respect.

An emaciated adult male that came into the clearing just before he died had a large open wound in his side in which were imbedded 120 primary maggots, *Cochliomyia hominivorax* Coquerel. These may have been the cause of death. There were 74 ticks, *Amblyomma ovale* Koch, attached to his skin. He also had cestodes in his

stomach and small intestine, and acanthocephalans in his large intestine and rectum. A juvenile male which died in captivity had trematodes and cestodes in his intestine. The infestations of internal parasites were apparently not heavy enough to cause the death of either coati.

I am indebted to Frank Radovsky and Richard Garcia, graduate students in the Department of Entomology and Parasitology at the University of California, Berkeley, for identifying the maggots and ticks.

COMPETITORS

Because of the coatis' omnivorous habits, many other mammals compete with them for food. Some of these competitors, or at least their young, are also potential prey for the coatis. Encounters were observed between coatis and a few of their competitors.

Armadillos (*Dasypus novemcinctus*) feed on small invertebrates in the litter, and frequently leave collections of small pits in the ground which resemble those dug by coatis. Agoutis (*Dasyprocta punctata*) often feed under fruit trees with coati bands, and squirrels (*Sciurus granatensis*) feed on many of the same fruits. Most of the time the coatis ignored these animals when they met, and even when they were feeding together. Once in a while a young coati showed some slight interest in one of them and went closer to investigate, and occasionally an adult chased an animal that was already moving away. But when an armadillo was overtaken, the coati soon slowed down and turned back. None of these "chases" represented a serious attempt to catch the other animal, and they seem to indicate merely that coatis often run after any relatively small thing that moves away from them. Armadillos, agoutis, and squirrels usually paid no attention to the coatis except to move aside if a coati approached very close. One agouti rapped on the ground with both hind feet simultaneously when an adult coati wandered by, then carried the fruit it was eating off about twenty feet to finish it.

White-faced monkeys (*Cebus capucinus*) were the only mammals that went out of their way to make contact with coatis. Sometimes the two species ignored each other, but several times coatis feeding in fruit trees were seen to return to the ground when a group of *Cebus* arrived. The prudence of this act was made clear on other occasions when groups of these monkeys chased coatis out of trees (*Chrysophyllum*, *Scheelea*) in which they had been feeding. One troupe of monkeys continued dropping nuts and debris from a *Scheelea* palm on Band 3 after chasing M31 out of the tree, but the coatis ignored the shower except to pounce on and eat the ripe nuts that were included. Coatis were also harassed occasionally by *Cebus* troupes when no food was involved, and once when a group of *Cebus* ran by on the ground fifty feet from a coati band, most of the coatis ran off in panic.

Coatis and howler monkeys (*Alouatta villosa*, commonly referred to in the literature as *A. palliata*) fed together in the same fruit tree without incident on a number of occasions. Once a howler and a coati met on the same branch, and the howler yielded the right-of-way. Carpenter (1934) also saw howlers and coatis feed peacefully together in the same trees many times, and only once saw a howler chase coatis out of a tree. The coatis I watched never paid any attention to the full-throated roars of nearby howler clans.

Night monkeys (*Aotus trivirgatus*) and kinkajous (*Potos flavus*) compete with coatis for fruit in trees, but since both species are nocturnal they rarely encounter coatis.

Tayras (*Eira barbara*) may be considered as potential predators on coatis, but like coatis, tayras eat considerable quantities of fruit, and were seen several times feeding in *Cecropia* trees with coatis. Neither species paid any attention to the other.

Collared peccaries (*Tayassu tajacu*) and tapirs (*Tapirus bairdii*) compete with coatis for fallen fruit. In frequent encounters peccaries sometimes filed through bands of coatis (once within six feet of me) and on one occasion fed beneath the same hogplum tree (again within six feet of me). They ignored me and the coatis impartially, and the coatis ignored them, except to step aside when directly in a peccary's path. Peccaries also root in the litter and may compete with the coatis for the invertebrates found there. White-lipped peccaries (*Tayassu pecari*) have not been seen on the island in recent years but would compete with the coatis in the same ways as the collared peccaries.

Wild tapirs have apparently been exterminated by poachers on Barro Colorado. An introduced tame tapir feeding on fallen figs near a band occasioned only mild curiosity and very mild alarm from a few coatis. Most of them ignored him.

RELATIONS WITH OTHER VERTEBRATES

Coatis frequently encountered other vertebrates that cannot be considered competitors, but which evoked some unexpected reactions.

The only snake I saw encountered naturally by a band of coatis—a two-foot coral snake (*Micrurus nigrocinctus*)—was ignored after a passing sniff. A three-foot vine snake (*Oxybelis aeneus*) and a five-foot unidentified red-and-black colubrid evoked only mild alarm and curiosity when presented to Band 1 on separate occasions, and the coatis soon lost interest. One subadult male apparently forgot about the colubrid as he foraged near it and walked right over it. It struck him on the leg, and he jumped two feet up and back but paid no further attention to it. None of the coatis attacked any of these small snakes.

Turtles often evoked a surprisingly strong alarm reaction. A subadult female came upon a three-inch turtle, grunted, and started back suddenly. I called several others of the band over, and when they got within two or three feet they too grunted and jumped back. This reaction was seen on several other occasions in juveniles or subadults. Adult female coatis usually ignored turtles, though one did sniff at a nine-inch specimen and turned it around with her paw. I never saw a coati attack a turtle.

Once a group of coatis responded with mild alarm to the loud call of a rufous motmot (*Baryphthengus ruficapillus*) that was excited by the presence of a spectacled owl (*Pulsatrix perspicillata*) in a nearby tree. The coatis had not seen the owl. On other occasions coatis were alarmed by the alarm calls of agoutis and the loud chattering of squirrels.

Coatis usually ignored anteaters (*Tamandua tetradactyla*), but one young male chased an anteater across a log, up a tree, and back down again before he lost interest and allowed the anteater to hurry off unmolested. Both animals were silent

during the encounter, as was usual in encounters between coatis and other species. Coatis fed unconcernedly near brockets (*Mazama americana*) and white-tailed deer (*Dama virginiana*) after some initial curiosity and/or alarm when they appeared.

HOME RANGE, MOVEMENTS, AND POPULATIONS

HOME RANGE

REVIEW OF CONCEPTS

Home range was defined by Burt (1943) as that area normally traversed by an individual in its day-to-day activities of food-gathering, mating, and caring for young. The home range is limited and constant for a given period of time, and does not include the areas covered on occasional long forays of a possibly exploratory nature. He defined territory as any defended part of the home range. These concepts have been widely accepted by mammalogists, and numerous methods for measuring home ranges and determining their patterns of use have been developed. Mammal studies involving direct observation of home range use are rare, and have concentrated on such larger species as wolves (Murie, 1944), foxes (Scott, 1943), deer (Dasmann and Taber, 1956), vicuña (Koford, 1957), and monkeys (Carpenter, 1934). Most home range studies are based on the recapture data obtained from small mammal studies, and various characteristics of mammal home ranges and their patterns of use have been assumed or discovered by a number of workers. These were summarized and compared by Hayne (1949) and Stickel (1954).

Hayne (1949) also first suggested the use of a geometrically determined "center of activity" (the geographical center of all of the points of observation or recapture) as a tool for indicating the distribution of individuals in an area, for detecting shifts in activity in the home range or shifts in the home range itself, and for indicating the size of the home range. The use of the activity center concept for expressing home ranges with indefinite boundaries and the density of small mammals on such home ranges statistically was further developed by Dice and Clark (1953) and Calhoun and Casby (1958). Odum and Kuentzler (1955), working with data on bird territories, successfully tested the method of Dice and Clark for indicating the presence of defended territories with fixed boundaries. Underlying all of these statistical manipulations is the basic idea, expressed by Dice and Clark, that because mammals with undefended home ranges have no fixed limit to their wanderings, attempts to fix boundaries of home ranges, i.e., to express home range as an area, are futile. They suggested instead that home range be expressed in terms of an "activity radius," based on the distance of recaptures from the "recapture center" (an approximation of the activity center). It was suggested by Calhoun and Casby that the home range and density of nonterritorial mammals is best expressed by a statistical measure of the probability of finding the animal at varying distances from the center of activity. However, Dasmann and Taber (1956) felt that the nonterritorial black-tailed deer, which they watched, had true home ranges with definite limits, and that boundaries and areas for these home ranges gave a truer picture than would the activity radii suggested by Dice and Clark. Finally, Pitelka (1959) emphasized the functional significance of "terri-

tory" in spacing out the individuals of a species, and advocated the use of the term, without regard to the method, behavioral or otherwise, by which exclusiveness is maintained, for areas of which at least parts are used exclusively by one member or social group of a species. The home range data obtained by direct observation of the Barro Colorado coatis in general supports the conclusions of Dasmann and Taber, and of Pitelka.

HOME RANGES OF BANDS

Most of my intensive observations were made in the area shown in figure 10. This area includes the complete home ranges of Band 1, 3, and 4; part of the known range of Band 5; and the location of the food station (Fairchild 6-7) where I observed Band 2. Such designations as "Fairchild 6" and "Lutz 2" refer to numbered stakes located approximately every 100 meters along the trails. These 100 meter sections are indicated on the maps.

The daily wanderings of Bands 1, 3, 4, and 5 were mapped an average of eight or ten times a month in the period of observation for each band. It was soon evident that each band confined its movements to a definite home range. The home range maps presented for Bands 1, 3, and 4 (figs. 11-13) were compiled from all of the daily route records collected for each band for periods of eight, seven, and seven months respectively. Because Band 5's movements were followed closely for less than two months, no home range map is presented, but the movements charted during that period give a fair approximation of the most used portion of the range.

The boundaries of the home ranges represent composites of the actual routes followed by each band in their farthest observed wanderings; they are not simply lines connecting isolated points as are those obtained by the usual trap-recapture or repeated observation methods. This procedure is illustrated in figure 14, which shows all of the plotted movements of Band 4.

These marginal wanderings were not single rapid forays directly out of and back into the core area of the home range, but parts of long, leisurely loops that began and ended (either on the same or the next day) in different parts of the core area. All or part of many of these longer loops were repeated at least once. Some of the longer loops were repeated months later; others were repeated frequently in a short period while a particular fruit crop was available. They indicated not a permanent shift of the home range during the period of observation, but rather irregularly visited extremes of the home range. To this extent the ranges fit the "indefinite" type of home range described by Dice and Clark, and by Calhoun and Casby.

However, several considerations incline me to treat these as definite home ranges that can be expressed usefully, though admittedly not absolutely, by areas and boundaries. Even when temporarily using distant parts of the home range, as when a particular fruit was available, the coati bands observed the new limits repeatedly. Apparently the adult females, at least, had been there before and knew the area, including the location of the fruit trees. While within the boundaries that I have drawn, the bands fed and moved with no sign of uneasiness or unfamiliarity. In contrast to this was the behavior of Band 4 on January 23, 1960. They were feeding, traveling along spread out and at a normal pace, near the

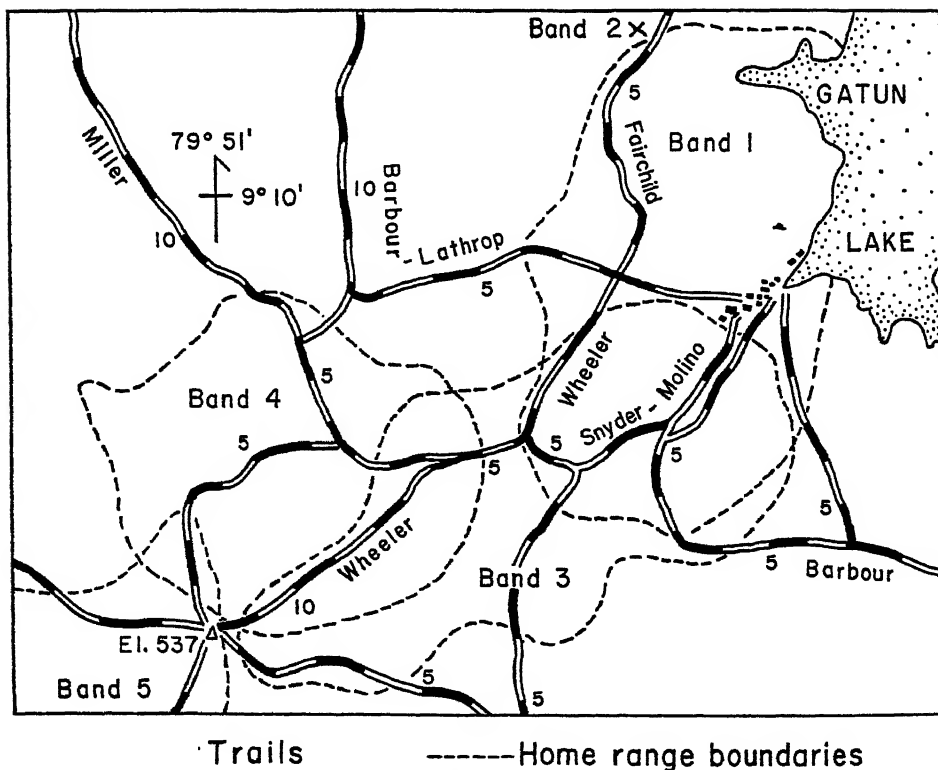
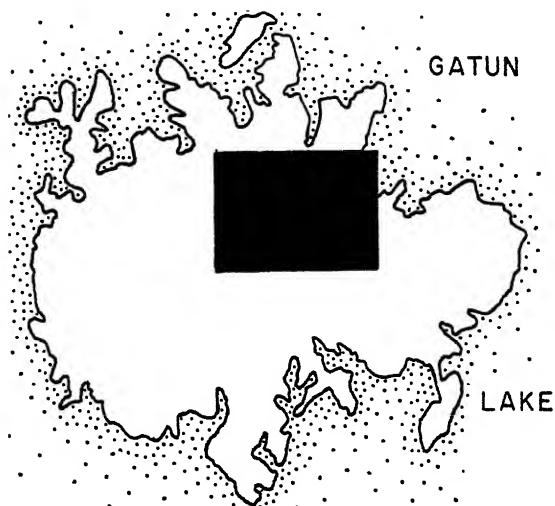


Fig. 10. Barro Colorado Island. The black area, enlarged below, is the area of intensive study. Trails are marked off in 100-meter sections, which are numbered on the map every 500 meters. The laboratory clearing is located on the cove on the east side of the island. Band 2 was observed only at the food station marked by the X near Fairchild 6.

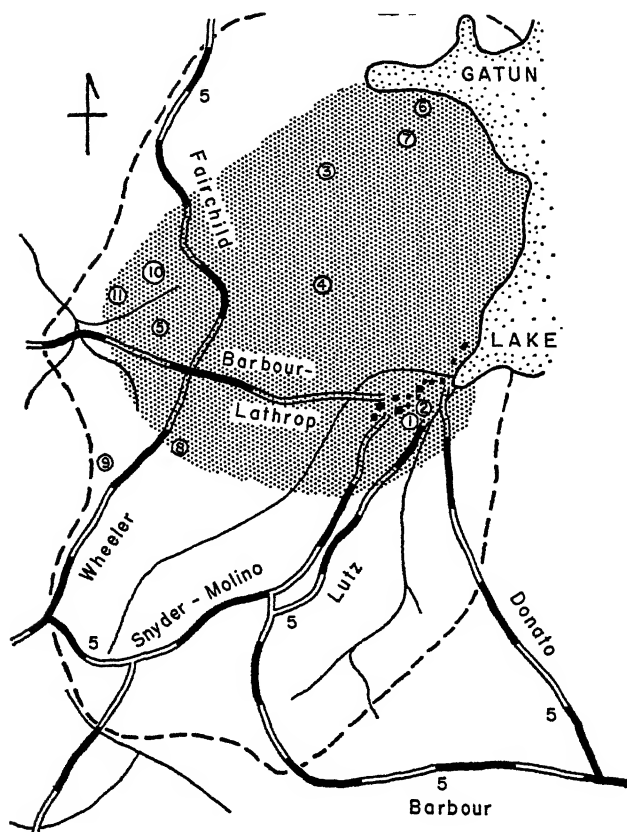


Fig. 11. Home range of Band 1. Trails are marked off in 100-meter sections, which are numbered on the map every 500 meters. The circled numbers refer to the roost trees listed in table 1. Broken line indicates the boundary of the home range. The core area is shaded.

northwest boundary of their range, accompanied by MSf. On reaching the connecting trail between Miller 6 and Barbour-Lathrop, several moved northwest more or less along the trail. The others followed, and soon the whole band was beyond the limit of their home range. When they reached Barbour-Lathrop trail they stopped feeding in the litter and seemed confused and panicky. They bunched into a tight group and dashed up Barbour-Lathrop trail, tails erect, for about fifty meters. Then they ran back and forth on both sides of the trail, still bunched up. Finally they turned back the way they had come, reentered their home range, and returned to their normal pattern of feeding and moving. Twice pairs of coatis from Band 1 were followed briefly just outside of their home range, and on both occasions they ran back and forth constantly in an uneasy manner.

Odum and Kuentzler (1955) suggested a distinction between "maximum" and "utilized" home range. The boundaries of the maximum home range are formed of straight lines connecting the extreme outermost observed points so as to include

all other points, and the writers offered a standardized statistical method for determining this maximum range. The utilized home range is that part of the artificially delimited maximum home range that the animal actually uses, and cannot be accurately determined by their method. Because in the present study the boundaries of the home ranges are composed of segments of actual movements of the bands, and the areas enclosed within these boundaries were covered by other movements at various times, the maximum home ranges are identical with the

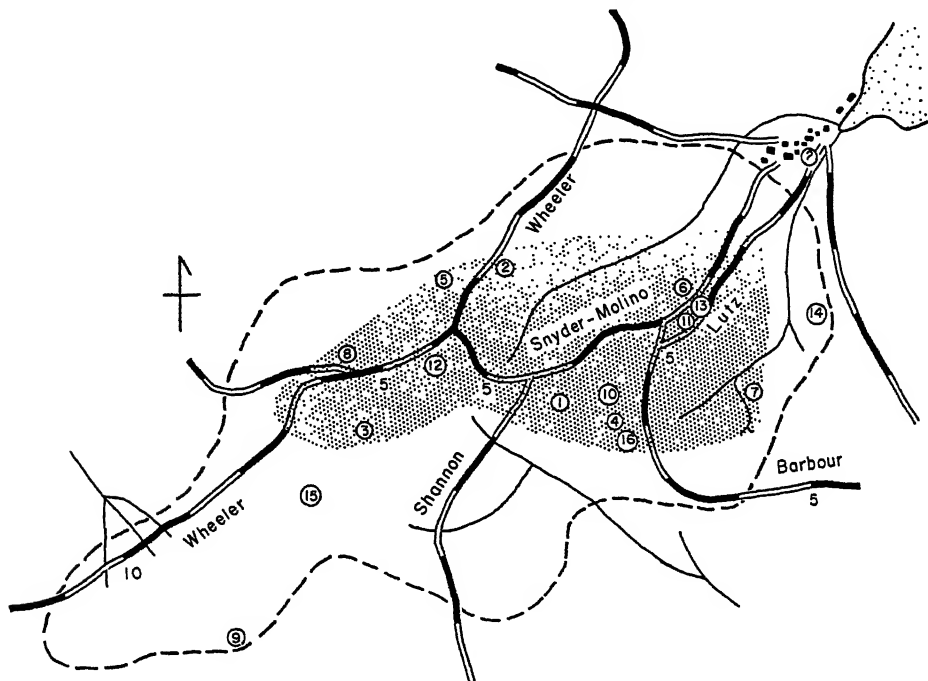


Fig. 12. Home range of Band 3. Trails are marked off in 100-meter sections, which are numbered on the map every 500 meters. The circled numbers refer to the roost trees listed in table 1; the roost tree indicated by "?" was probably used by this band. Broken line indicates the boundary of the home range. The core area is shaded.

utilized home ranges. Limiting the maximum home ranges by the method of Odum and Kuentzler would result only in smaller, still fully utilized ranges that would not include some significant seasonal extensions.

Core areas.—Of greater significance than the maximum (utilized) home range, the limits of which depend to some extent on particular fruit crops, is a constantly used central area within the home range of each coati band. It has been generally assumed that some area within the home range of each animal or social group is used more frequently than any other, and that this area probably contains the principle home sites and refuges and the most dependable food sources. Hayne's activity center is an arbitrarily determined approximation of the focus of such an area, and some evidence of preferential use of the home range was produced by the studies mentioned earlier in which larger mammals or their tracks were observed directly.

I have already referred to the "core area" of the coati home ranges. This was the area of heaviest regular use throughout the entire period of observation, and was determined by inspecting the daily route maps for each band. Such areas of heavy temporary use as the western part of Band 4's range, which was visited frequently while the almendro trees there were in fruit but not before or after, were not included. Within each core area, the routes form a dense, tangled skein of tracings (see fig. 14). Outside of the core area, activity was conspicuously less concentrated.

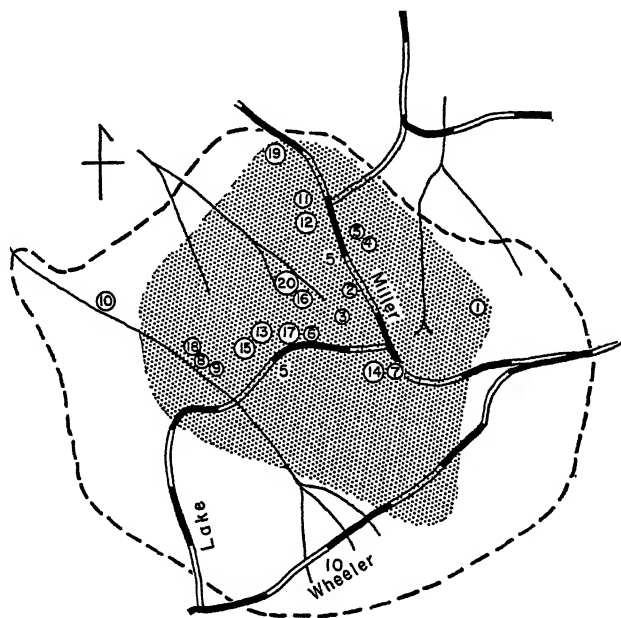


Fig. 13. Home range of Band 4. Trails are marked off in 100-meter sections, which are numbered on the map every 500 meters. The circled numbers refer to the roost trees listed in table 1. Broken line indicates the boundary of the home range. The core area is shaded.

Even during those periods when areas outside the core area were temporarily receiving heavy use, the bands spent part of each day in the core area and almost always retired to a roost tree within the core area. Of 47 known roosts for the three bands, only 5 were outside of core areas, and 2 of these were in, or adjacent to, large trees in fruit.

Band 3 served as a useful check on the possibility that the heavy use of the core areas was an artifact caused by the presence of food stations. Band 3 was never baited, and it followed the same pattern of home range use as did Bands 1 and 4.

On three occasions a pair of juveniles (m32, f37) was separated from Band 3, and each time they returned to the same small area within the core area where they waited until the band came by. On November 20 and December 13, 1958, I found them alone in the area between Snyder-Molino 2 and Lutz 4. They remained there until picked up by the band later the same day. Their mother disappeared on December 15, and on December 18, m32 and f37 lost contact after dark just before

the band retired to roost tree #9, near Balboa 4. Five days later m32 turned up, alone and badly gashed, in the Synder-Molino 2-Lutz 4 area and was picked up by the band there; f37 was not seen again.

After the core areas had been outlined on the maps, their areas and those of the full home ranges were determined with a planimeter. The time spent by each band in its core area was then computed, and compared with the total time of observation for each band. These figures are presented in table 7.

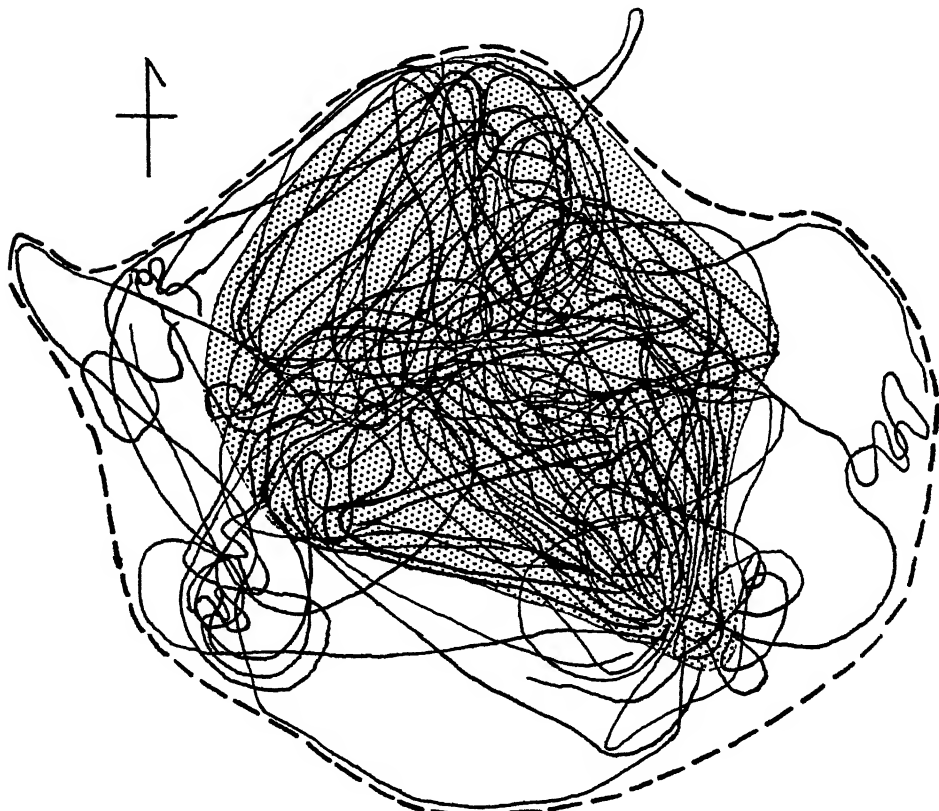


Fig. 14. All observed movements of Band 4, October, 1959, to June, 1960, showing the method of determining home ranges and core areas (shaded). The loop outside the home range to the north represents the incident described on page 169, when the band seemed to be temporarily "lost."

The significant feature of these figures is not the approximate size of the home ranges, but rather that about 80 per cent of each band's time was spent in a core area which included only about 40 per cent of the home range.

Effects of succession.—The actual ground area of each range is somewhat larger than indicated, owing to the hilly nature of the terrain. Furthermore, the tropical forest is very much a three-dimensional habitat, and the range of any animal with arboreal tendencies is also three-dimensional. Band 1's range was in an area of relatively early succession, with few really large trees. Most of their considerable wanderings from the core area were trips to such preferred large fruit

trees as figs and hogplums. They did have the benefit of several species of second-growth trees with good fruit crops, such as *Cecropia* and *Coussarea*. The ranges of Bands 3 and 4 included areas of somewhat more mature forest with more large fruit trees. Of the bands followed, only Band 5 was in an area of truly mature forest, and not enough data were collected on this band to shed any light on possible differences in home range size or on the extent of daily and seasonal movements. The possible qualitative and quantitative differences in the litter fauna in areas of different successional development are completely unknown, and are quite possibly more important than the presence of fruit trees, since the coati's diet is composed almost entirely of litter animals for most of the year.

TABLE 7

COMPARISONS OF THE AREA OF HOME RANGES AND CORE AREAS AND THE TIME SPENT IN EACH

Part of range	Area to nearest hectare (and in acres*)	Per cent of entire home range	Hours observed*	Per cent of total hours observed
Band 1				
Home range.....	45 (110)	100	300	100
Core area.....	20 (50)	44	245	82
Band 3				
Home range.....	41 (100)	100	435	100
Core area.....	15 (35)	37	355	82
Band 4				
Home range.....	34 (85)	100	435	100
Core area.....	15 (35)	44	350	80

* Rounded to the nearest 5.

Overlap.—There is considerable overlap in the ranges of individual bands, as shown in figure 15. The ranges of Bands 4 and 5 overlapped, and other bands were seen from time to time within the home ranges of all of the bands followed. This was especially true in areas with large trees in fruit—several bands may include such areas in the peripheral part of their home ranges and visit them frequently during the fruiting season. In all, twenty-two encounters between different bands were observed, ten of them between Bands 1 and 3. (The relations between bands are discussed more fully in the section on social behavior, but it should be noted here that there is usually little or no friction when bands meet, even within the core area of one of them.) However, the core areas of the bands did not overlap, and because each band spends eighty per cent of its time within its core area, band-to-band encounters are not very frequent, and effective spacing of the population is achieved. Thus the core areas fit Pitelka's definition of "territory" quite well, even though they are not defended. There is possibly a direct connection between the lack of territorial defense and the socially subordinate position of the males.

Seasonal variation in use of home range.—The core areas were used consistently throughout the periods of observation, but some of the peripheral areas of the home ranges were visited only while certain fruit crops were available. Band 1 visited the southwestern extremities of its home range only while hogplums and figs were in fruit there during September and April, respectively. Band 3 visited the areas near Donato 3 and Shannon 4 only to feed on figs during January and

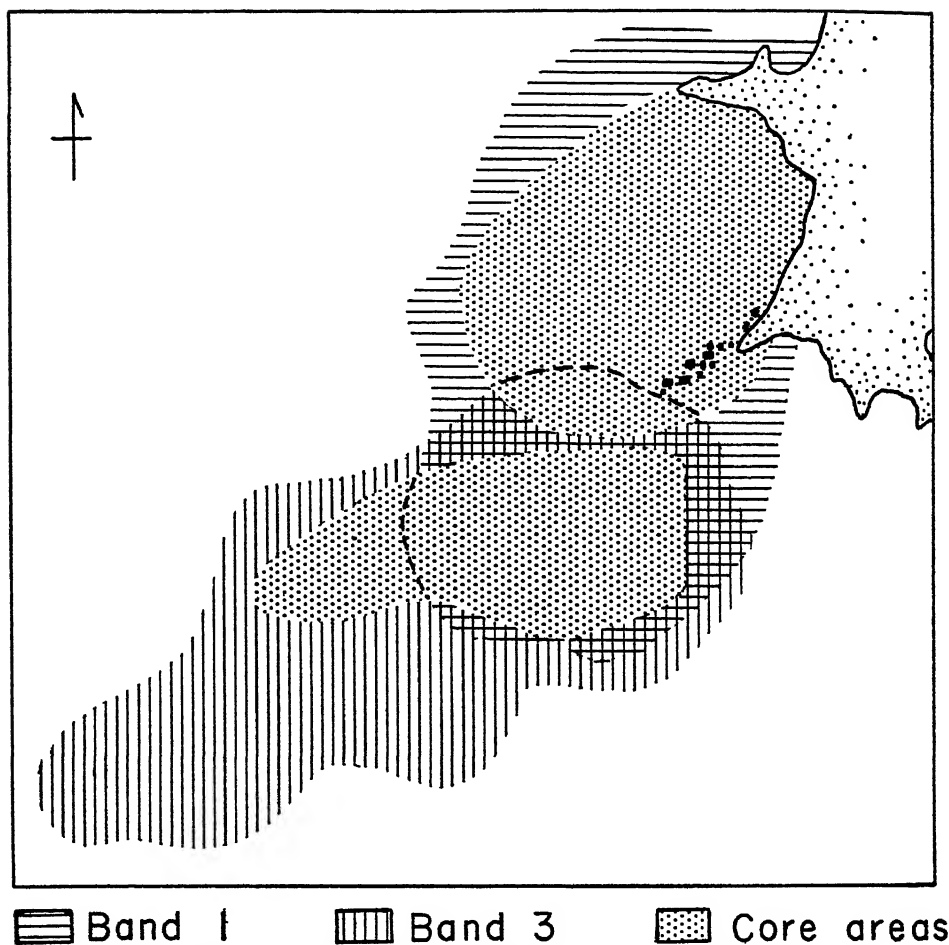


Fig. 15. Overlap in ranges of Bands 1 and 3. Note that the core areas do not overlap.

March, and Band 4 visited the peripheral areas of its range almost exclusively to feed on almendros during the dry season. Maps of the principal fruit trees in each of the home ranges are included in the section on food habits.

During April, 1959, Band 1 ranged more widely than usual, which may have been a reflection of a shortage of food. I lost contact with them at the end of the month, and although they were seen within their usual range from time to time after that, they may have partly shifted their home range. Other considerations add to the uncertainty at this period: the gradual departure of the newly adult males, and a possible temporary break-up of the rest of the band despite the fact that none of the females bore young.

SOLITARY ADULT MALES

Because adult males could not be followed successfully, I have very little data on the extent of their home ranges, or on their movements within the ranges; however, repeated observations of known individuals have provided some information.

Adult males as well as bands apparently have home ranges, since individuals were seen regularly and repeatedly in the same areas. MSa and MSd were both seen frequently near the laboratory during the first year of the study, and the sightings indicate ranges with minimum lengths and widths of 600×600 meters and 650×700 meters, respectively. There is no way of telling how far adult males may wander, but that they do so is indicated by a sighting of MSb 900 meters from his usual post in the laboratory clearing. MSf was frequently seen in the home range of Band 4, and during the mating period covered their entire range while traveling with them—an area with dimensions of 650×700 meters. How far he may have roamed at other times is not known.

Although I suspect that solitary males may wander more at times than do the bands, they are also more prone to take advantage of good food sources by settling down in a restricted area. Several such males were seen regularly in the laboratory clearing, where food was abundant, and apparently spent most of their time there. Other adult males made a habit of staying close to the artificial food stations while they were being supplied, and could usually be counted on to appear soon after the food did. However, the simultaneous possibility of frequent wanderings of considerable length is pointed up by the already-mentioned sighting of MSb, the most persistent of the clearing habitués.

The ranges of the solitary males who lived in and near the clearing overlapped each other extensively, and a similar overlap was observed in the ranges of MSf and MSg in the area of Band 4's range. The males do not defend any part of their ranges from other males, but usually do have some sort of brief contest (most often vocal, occasionally physical) when they meet at close range. The regular visitors to specific areas tolerate each other better, and several may feed close by each other with only occasional signs of friction.

RELEVANT DATA ON OTHER MAMMALS

Almost nothing is known of the size of home ranges of mammals in tropical forests. D. E. Davis (1945) found in Brazil that females of the common opossum (*Didelphis marsupialis*) stayed within an area with a diameter of 400 meters for 11 months, and that the ranges overlapped. Males apparently wandered more, since of 5 marked and released, only 2 were recaptured. Davis also presented information on the home ranges of smaller opossums, and of 3 species of mice. But the only detailed data on the home range of a tropical forest mammal that compares in size and social organization with the coatis are those provided by C. R. Carpenter (1934) for the howler monkeys (*Alouatta villosa* = *A. palliata*) on Barro Colorado. One social group of 25 to 35 howlers was observed 73 times in 5 months (parts of successive dry seasons) and had a home range that was approximately circular, with a radius of about 600 yards and an area of about 300 acres. This group's range overlapped that of another group of about the same size, but with a smaller home range. Carpenter states that the probable reason for their smaller range was that this second group lived in an area of taller, denser forest.

Information on the home range of another member of the Procyonidae—the northern raccoon (*Procyon lotor*)—was collected by Stuewer (1943) in a study in Michigan involving extensive live-trapping. The longest diameters of known

ranges of 19 adult males averaged one mile, with extremes of up to two miles; 17 adult females had ranges with an average diameter of .7 miles, with extremes of up to 1.4 miles; and 27 juvenile males and 24 juvenile females had ranges with average diameters of .7 miles and .5 miles, respectively. The ranges of males and of females with young overlapped, and twice pairs of dens were located only 600 feet apart.

Butterfield (1944) reported on the results of trapping raccoons in Ohio. Of 91 raccoons retrapped in periods of up to two years, none was taken more than one mile from the original trap location, and the average movement recorded was slightly less than $\frac{1}{4}$ mile.

PATTERNS AND LENGTHS OF MOVEMENT

Patterns of movements.—Coati bands typically spread out while moving and feeding, some of the members being as much as 100 meters apart at times. Although usually the spread is less, the members of a band are often out of sight of each other, and may be in any arrangement.

Except during brief periods of actual running, coatis feed in the litter almost constantly as they move. They may stop feeding while going up or down a steep slope, but they frequently fed along the steep sides of ravines where I had trouble following them. There is no general tendency to follow contours, streams, or trails, though all of these are at times followed for distances of up to several hundred meters. Fallen trees are often used in crossing ravines and negotiating steep slopes.

The bands move freely over their ranges without any consistent pattern. Figure 16 shows four different routes of daily movement for Band 1. Sometimes their movements are direct and they cover relatively long distances in a few hours; at other times they circle repeatedly in a small area for anywhere from a few minutes to all day, often to eat ripe fruit on the ground. Coatis also may spend an hour or more searching in large patches of piñuella plants for insects. Sometimes they mill around simply feeding in the litter when no special attraction is apparent. Arboreal feeding may also delay progress for periods varying from minutes to hours.

Even on the more sustained marches, progress is variable. For long periods the bands move fairly steadily, feeding in the litter as they go. The maximum rate attained at such times is about 300 meters per hour, but this pace is seldom maintained for long. These progressions are occasionally interrupted by periods of more rapid movement, with frequent short intervals of running without feeding. Some brief spurts of running have an obvious cause, such as a loud noise, but others seem spontaneous to an observer lacking the sense organs of a coati. More extended periods of rapid movement also occur and are especially typical of "uneasy" animals: bands in the rain, individuals or small groups isolated from the band, bands not accustomed to the presence of an observer, etc. Once the bands became accustomed to being followed, and I had become familiar with the terrain, I was in little danger of losing contact.

Lengths of daily movements.—The distances covered by Bands 1, 3, and 4 in their daily movements are summarized in figure 17 and table 8. These distances were measured from the daily routes plotted on maps, and represent minimum net

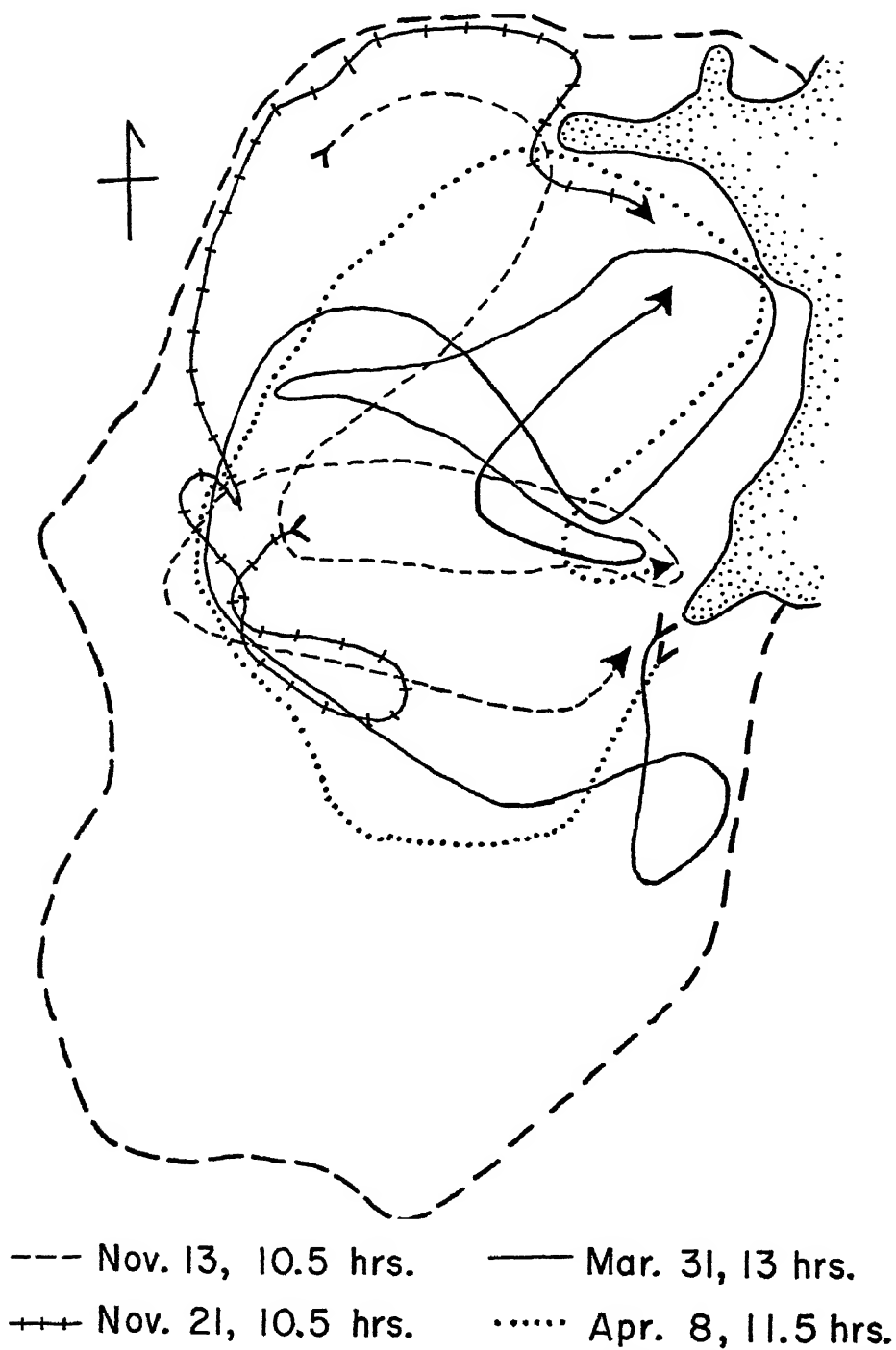


Fig. 16. Selected daily routes of Band 1, 1958-1959, showing typical patterns of movement.

movements of the whole group between landmarks (mostly trails) that could be located on maps. There was no way to measure the intricate, twisting paths actually followed by the animals, and the actual distances traveled are much greater than those shown. A pedometer on my own belt was of no use because I could not standardize my paces while keeping with the bands.

Table 8 is compiled from all of the data on movements obtained from following these bands in the periods indicated. The total distance covered was divided

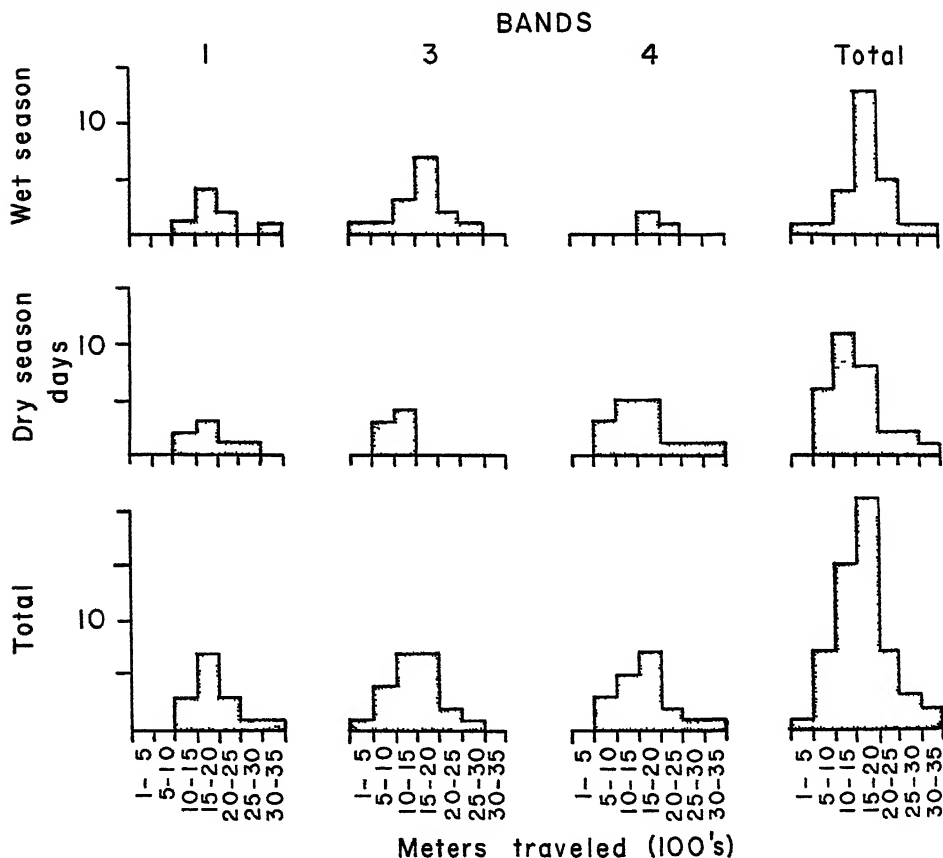


Fig. 17. Length of daily movements of Bands 1, 3, and 4, based on days for which continuous observations were made for at least 8 hours. Figures have been adjusted to a standard 12-hour day.

by the total time of observation to get a rate, in meters per hour, that includes all of the coatis' activities: moving, resting and grooming, and feeding in one place. This over-all rate was then multiplied by 12 to get a standardized approximation of a full day's travel. There was close agreement between the distances thus computed and the actual distances covered during days when I was with the bands from dawn to dark. Figure 17 includes data only from those days when I was with the bands continuously for 8 hours or more. For comparison, each daily total was adjusted to a standard 12-hour day (e.g., distances covered in 10 hours were multiplied by 12/10).

The length of daily movements for the three bands was most often between 1,500 and 2,000 meters. Each band made shorter daily movements in the dry than in the wet season, correlated with the increased amount of resting in the dry season. There was also some variation among the bands in average distances traveled daily; Bands 1 and 4 went farther than Band 3, even in the dry season, when Band 3 rested less, only 8 per cent of the time, than Bands 1 and 4, with 18 and 14 per cent respectively. The difference between the average daily movements of Bands 1 and 4 during the dry season is largely due to the availability of concentrated fruit crops to Band 4.

TABLE 8
AVERAGE LENGTH OF DAILY MOVEMENTS

Band	Hours observed	Total movement in meters ^a	Average day's movement in meters ^a (meters per hour \times 12)
WET SEASON			
Band 1.....	162 5	28,950	2,150
Band 3.....	250 5	33,250	1,600
Band 4.....	72	13,250	2,200
All.....	485	75,450	1,850
DRY SEASON			
Band 1.	133	19,800	1,800
Band 3	150	15,850	1,250
Band 4 ^b	243 ^b	30,100 ^b	1,350 ^b
All.....	526	65,750	1,500

NOTE: Longest day's movement observed: 3,350 meters in 11.5 hours with one 25-minute rest period, Band 1, September 13, 1958. Shortest day's movement observed: 100 meters in 9.5 hours with no long rest period, Band 3, September 27, 1958.

^a Rounded to the nearest 50.

^b Band 4 data only through April 1.

C. R. Carpenter (1934) followed a clan of howler monkeys on Barro Colorado for 30 consecutive days in January, 1933. Their average daily movement was about 200 meters, with a minimum of 50 meters and a maximum of 800 meters.

POPULATION DENSITY AND FLUCTUATION

Density.—Because of violent fluctuations in the numbers of coatis in bands in the course of this study, and because adult males are hard to census, I had difficulty compiling any meaningful expression of density on even that part of the island in which I worked intensively. Table 9 presents density figures for bands in their core areas and for all coatis definitely known to be living in the entire home ranges. The contemporary overlapping ranges of Bands 1 and 3 are combined. There were quite possibly more adult males present in these areas than I have indicated, especially in the vicinity of the laboratory clearing, where the solitary males congregated. (There were at least nine such males around the clearing in June, 1960). Since the solitary males tend both to wander and to settle at least temporarily in areas where food is plentiful, any census of them in a small area at a given time

can be only a rough approximation. For this reason, the figures presented here should be taken only as an indication of the order of magnitude of the coati populations in these areas. As an index to the relative density of coatis in bands, figures based on the core areas only are perhaps more significant than those based on the more variable overlapping home ranges.

Butterfield (1944) reported densities for raccoons in Ohio of from 1/11.7 acres to 1/106 acres, depending on habitat and hunting pressure.

Fluctuation.—The coati population that I watched on Barro Colorado suffered a great decrease in late 1958 and early 1959. When I arrived on the island in July, 1958, coatis were common everywhere, and I soon had two bands that could be

TABLE 9
DENSITY OF COATI POPULATION IN CORE AREAS AND ENTIRE HOME RANGES
(Census taken in October of both years listed.)

Band	Core area density per 10 hectares ^a	Entire home range			
		Number in band	Minimum number adult males	Total number	Density per 10 hectares ^a
Band 1 (1958)	6.5.....	13 ^b	}	28	4.2
Band 3 (1958)	6.0.....	9 ^c			
Band 4 (1959)	4.7.....	7 ^d	2	9	2.6

^a Equals 25 acres.

^b Includes 2 juveniles.

^c Includes 4 juveniles.

^d Includes 3 juveniles.

followed. In the ensuing months, however, they dwindled away, making it necessary for me to locate other bands for the second year's work. In September, 1958, there was a total of 7 juveniles in the two bands; by the following May only 1 was still alive. Of 6 adult females, 1 survived; of 7 subadult females, 4 survived. The 4 subadult males in the two bands survived, and at least 3 of the 4 adult males also survived this period. Neither band produced offspring in 1959, and fewer coatis were seen on the island in the second year of the study. Band 5 dwindled similarly during the latter part of 1959 and was abandoned early in 1960. Band 4, however, suffered no losses between October, 1959, and April, 1960. At least 10 new young were born in April, and on June 4, 8 of these were still alive. The losses for Bands 1, 3, and 4 are summarized in Table 10.

There is no reliable way to census coatis in a large area, but a rough estimate of 400 to 600 can be made for the entire island, based on a comparison of the total area of the island with the area for which I have density figures. The actual number apparently varies considerably from year to year (the population I was watching decreased by 50 per cent in 8 months), which leads to the conclusion that populations of tropical mammals may fluctuate more than is generally believed. Further support for this conclusion comes from the periodic censuses of howler monkeys on Barro Colorado. Because of their limited mobility and convenient habit of howling at dawn, howlers are ideal subjects for a census. Table 11 summarizes the

TABLE 10
MORTALITY IN 3 COATI BANDS

Month	Number alive at end of month		
	Band 1 (1958-1959)	Band 3 (1958-1959)	Band 4 (1959-1960)
Aug.....	15
Sept.....	13	9	..
Oct.....	13	9	7
Nov.....	13	9	7
Dec.....	13	7	7
Jan.....	9	3	7
Feb.....	9	3	7
Mar.....	9	3	7
Apr.....	8 ^a	2 ^b	17 ^c
May.....	8 ^a	..	17
June.....	8 ^a	..	15 ^d

^a Three 2-year-old males leaving band, 5 females still in band.

^b Two survivors join remnant of another band.

^c Minimum; young still in nests.

^d Maximum; not seen after June 4.

findings of C. R. Carpenter (1934), Collias and Southwick (1952), and Carpenter, Southwick, and Mason (personal communication from Dr. Carpenter, 1961).

The size and composition (by age and sex groups) of the howler monkey clans was approximately the same in 1932, 1933, and 1959; as the total population increased, more clans were formed. The population decrease reported for 1951 (which may have been caused by a yellow fever epidemic) resulted in a reduction of the clans to half their "normal" size, but there was no decrease in the number of clans from 1933. Chapman (1929) reported that the coati bands had from 15 to 40 members each. This estimate, if accurate, would indicate a much larger population than was present in 1958-1960, when the bands were much smaller, with an observed maximum of under twenty individuals per band, and an average October band size of about ten. This sort of speculation tells us only that we are greatly in need of careful counts of tropical mammals—or at least of indices of population changes.

Not even the immediate causes of death, much less the underlying causes of these fluctuations, are known. Coatis have remarkable powers of recovery from physical injury; gaping wounds were observed several times in both juveniles and adults, but seemed to cause no trouble and healed clean in a few weeks. However,

TABLE 11
SUMMARY OF HOWLER MONKEY CENSUSES ON BARRO COLORADO

Year	Total number of monkeys	Number of clans	Average number per clan
1932.....	398	23	17.3
1933.....	489	28	17.4
1951.....	237	29	8.1
1959.....	814	44	18.9

such widespread disorders as hunger, the psychological effect of overcrowding, or an organic disease could cause general weakness that would result in deaths from a number of immediate causes—injuries, internal parasites, etc.—which would ordinarily not be fatal. Most of the coatis simply disappeared, sometimes after appearing “sick” or “sleepy” for a few days. Some were never seen again; the bodies I found were too far reduced by decay, maggots, and vultures to be of any help in determining the causes of death.

The mechanism behind the fluctuations will probably not be discovered until much more is known about basic environmental influences. It would be interesting to know the effect on the litter fauna of recurring one-to-three year periods of unusual dryness (fig. 2), and the indirect effect they may have on animals that feed in the litter. If food in the litter should become scarce, the coatis would be hard-pressed, especially in years when the fruit crops were not large. Almendros and black palms, both mainstays in the first half of 1960, do not have large fruit crops every year and were not available in 1959. Enders (1935) and Chapman (1938) both commented on the scarcity of fruit during the 1932 dry season, apparently caused by very heavy rains during the flowering period the previous November. Coatis, peccaries, and opossums were all short of food, and Chapman presented photographic evidence of the poor condition of white-lipped peccaries during this period. That such shortages of food may occur periodically in a humid tropical forest might seem novel, but the possibility points up the need for more careful investigation and fewer careless assumptions if we are ever to approach an understanding of this complex habitat.

FOOD HABITS

Although the information on food habits that can be gained from direct observation is in some ways limited, the method has important advantages over the analysis of scats and stomach contents. Coatis usually swallow small litter animals before even a glimpse can be had of them, and guard their larger prey so well that it is an accomplishment just to know for certain whether it is a lizard or a crab being eaten. Thus no detailed lists of species or measured quantities of food animals can be compiled from direct observations. However, scats and stomach contents tell one little about timing and methods of search, procurement, killing, and eating. Pulpy fruits are more identifiable on or under the tree than in the stomach or feces. Direct observation often gives a truer picture of the relative importance of different food categories because seasonal and easily digested materials tend to be neglected in stomach and scat examination. Ideally, the methods should be combined. But collecting specimens for their stomachs is incompatible with a program of continuous observation, and there is no way of knowing how much the food habits of animals collected elsewhere differ from those in the area being studied. This problem is especially crucial with such an adaptable, opportunistic animal as the coati, and with such great variation in habitat as that between the island and nearby areas on the mainland. It is difficult to locate scats scattered at random in the tropical forest, and those I saw deposited added nothing to what I already knew from direct observation. Therefore, only information obtained by direct observation of wild animals is included in the following discussion.

ANIMAL FOODS

The animal foods that I observed coatis eating on Barro Colorado are summarized below.

ANNELIDA

Oligochaeta.—Earthworms are eaten from the litter.

ARTHROPODA

Crustacea.—A land crab (*Pseudothelphusa richmondi*) is abundant on Barro Colorado, ranging widely through the forest during the wet season and retreating to the streams in the dry season. Most of the crabs taken were found in the litter during the wet season: walking on the surface; under logs, piles of brush, or rocks; and in burrows. I saw 17 eaten in October, 15 in November, 6 in December, 1 in January, and 5 in April (after heavy rains).

Myriapoda.—Millipedes were eaten often, but no coatis were seen eating centipedes.

Arachnida.—Tarantulas (*Eurypelma*, *Sericopelma*) were dug from their burrows throughout the year. Smaller spiders were also frequently taken, and I saw 2 scorpions eaten.

Insecta.—Insects at all life stages were taken in all levels of the forest from litter to upper canopy. Orthopterans were among the most commonly caught: crickets in the litter, grasshoppers in small clearings, and katydids from all levels of the forest above the ground. Termites (Isoptera) were licked up from nests exposed in the litter on two occasions. Lepidopterans were frequently eaten, mostly larvae and pupae; I saw one adult *Morpho* captured and eaten. The multitudinous and ubiquitous Coleoptera are staples in the coati's diet. Of the Hymenoptera, I saw only ants eaten by coatis. These were licked up from nests in the litter on 4 occasions.

MOLLUSCA

Gastropoda.—Two species of snails, *Orthalicus princeps* (Broderip) and *Labyrinthus otis* Pilsbry, were eaten occasionally during the wet season.

CHORDATA

Amphibia.—Five specimens of *Caecilia ochrocephala* were captured on or just beneath the surface of the litter in the wet season. One large frog (*Leptodactylus pentadactylus*) was killed and eaten in November.

Reptilia.—The coatis I watched never showed any interest in snakes or turtles as food, but lizards were hotly pursued whenever they were encountered, and occasionally were dug from burrows. *Ameiva undulata* and *A. festiva* were the species most commonly seen in the forest litter, and these were the only species I saw eaten by the coatis (a total of 9 in 2 years).

Aves.—I never saw a coati rob a nest or catch a bird. Tinamous (*Timamus major*) and doves (*Leptotila cassinii*) feeding on the ground near a foraging band of coatis were ignored on several occasions.

Mammalia.—Small rodents were chased unsuccessfully on 4 occasions, and I saw only 2 mice eaten. Both were in burrows; one was dug out, the other was run down in the litter as it fled from a shallow burrow. A young agouti (*Dasyprocta punctata*) was chased by the subadult males in Band 1, but escaped down a burrow, and no effort was made to dig it out. An adult agouti was chased briefly by F42, but this was obviously not a serious attempt (see page 164). F51 was observed feeding on the remains of an agouti, but this was carrion-feeding and not predation. Coatis around the clearing also carried off the carcasses of a number of monkeys and a small ocelot which were placed under screens in the forest to be cleaned by maggots for skeletal preparations.

Some of these foods (crabs, snails, caecilians) are seasonal. Others, such as tarantulas, lizards, and small mammals, are available, and eaten, at all seasons. But nothing is known of the seasonal changes in the quality and quantity of the smaller invertebrate litter fauna, or of seasonal changes in the use of this crucial source of food.

LOCATION: SMELL VERSUS SIGHT

Coatis use a variety of methods in searching for various animals, and most emphasize the dominant role played by olfaction in receiving stimuli from a distance. Almost all animal food is initially located by constant sniffing in the litter and low plants. Small animals a foot or more in the ground or several feet above the surface are pinpointed in this way, and are directly dug up or extracted from under bark or leaves or from clumps of debris where they could not possibly have been seen. Frequently a coati will walk by an unseen morsel, sniff, and turn back to eat it. The possibility that hearing aids in the location of small animals in the litter cannot be discounted, although I did not observe coatis obviously listening as they searched for food.

When animals are flushed from the litter or low plants and fly or run away, they are followed by sight; but if, as commonly happens, they escape the initial rush, the search is resumed with the nose. When insects simply alight in the litter, there is sometimes a brief attempt, employing vision alone, to flush them by making a series of short pounces with the forepaws in the general vicinity where they were last seen. This, however, is often unsuccessful, and since larger animals head for more substantial cover, such as hollow logs and burrows, the excited sniffing begins again.

Artificial feeding produces similar results. Coatis accustomed to being fed continue to sniff in the litter at food stations, and do not go to plainly visible bread and bananas lying on the ground until their noses take them there. They watch when a small piece of bread is thrown and run to the spot where it falls, but frequently fail to notice it and walk past it. Eventually the food is located by more exploratory sniffing.

The searching techniques of an adult male and an adult female were tested separately by placing a banana six feet up in a tree. Both were aware of the bait and sniffed constantly, noses pointing up. They started about ten yards from the tree and seemed to be searching by trial and error at first. They walked around sniffing both at the ground and up in the air, then climbed several trees and vines for a few feet, sniffed in all directions, descended, and tried elsewhere. They moved slowly in the right direction until within two yards of the correct tree, then went directly to it and up to the fruit. Although they could obviously smell the banana from a considerable distance, they were unable to locate it precisely at a distance greater than about ten feet.

Chapman (1938) tested the ability of an adult male to locate bananas by suspending one from a horizontal wire 20 feet above the ground. The coati first located it by sniffing in all directions from the ground and climbing a short way up various trees until he found the one to which the horizontal wire was attached—a procedure similar to that used by the two coatis described above. After Chapman's male learned to retrieve the bait by walking the tight wire, he was able to detect the presence of a banana even when it was enclosed in a box, but he ignored the box when it was empty. He also ignored a carved, painted wooden banana when it was displayed alone and easily distinguished it from several real ones with a quick sniff.

These observations indicate that a coati's nose is quite an efficient sensory receptor, and that the eyes are relatively little used for locating food.

FORAGING METHODS

Coatis spend most of their waking hours feeding in the forest litter as they circle through their home range (pl. 12). They sniff along, pausing frequently to pick up small invertebrates with their teeth, or making short quick rushes to catch with the front paws those that flee. Rocks are turned, and sticks and palm fronds are turned over and ripped apart with the front claws. One solitary male was seen catching the crickets that were fleeing before an advancing swarm of army ants (*Eciton* sp.). Occasionally a lizard or mouse is scared up and a very excited chase ensues; often several members of the coati band join in the scramble before the prey is caught or, more often, escapes down a hole.

Coatis frequently dig small pits in the ground, from which they pick small arthropods neatly with the teeth, or scoop them out and eat them from the paw. Most of these pits are less than two inches deep and one to two inches in diameter at the top. Occasionally narrow pits up to thirteen inches deep are dug, from which perhaps several morsels are extracted at different stages of the digging. This is approximately the length of a foreleg of an adult, and these pits are just large enough to insert one foreleg (or the snout) at a time.

Table 12 and figure 18 show the results of counts of the number of small litter invertebrates eaten by coatis in five-minute periods. The counts were confined to periods of uninterrupted litter feeding in areas without heavy underbrush, and varied in length from five to twenty-five minutes. Only the tamest animals in the bands could be used for the counts, since it was necessary to stay very close to an individual in order to hear or see when something was eaten. Even then it was difficult to be sure, especially if more than one animal was taken from a single pit, so that the numbers of successes should only be taken as rough estimates. Furthermore, these counts give no indication of the actual biomass involved. Because of these large sources of error no comparisons will be made between counts made at different seasons, or in different areas.

Williams (1941) made a rough estimate of the biomass of the litter fauna on Barro Colorado in July. Using his own figures for the numbers of animals, and figures from a study in Illinois for the average weights of each group, he presented a figure of 15.53 grams per square meter, or about 138 pounds per acre. Williams states that these figures are too low for several reasons, but they do give an order of magnitude. His data suggest a greatly decreased density of litter animals at night, which could be due to their migration either down into the soil, or up into the plant strata. In either case, they would be less easily available to the coatis, which may be a major factor influencing the coati's diurnal rhythm.

Williams also found a rough positive correlation between litter moisture and the density of the litter fauna, and a gradual increase in the litter fauna during July. The latter data are only fragmentary, but they suggest a possible build-up during the early part of the wet season after a presumed low during the dry season. Dammerman (1925), working in a monsoon forest in the East Indies, reported a low in the litter fauna during the dry season and a high during the wet season.

TABLE 12
EFFICIENCY OF LITTER FEEDING

Sex and age of coati	Minutes observed	Number of successes*	Average per minute
Adult females (3).....	70	94	1.34
Subadult males (3).....	60	81	1.35
Juveniles (7).....	125	159	1.27

* Each litter animal eaten counts as one success.

Several factors, however, complicated the generally positive correlation between moisture and density of litter fauna.

None of the data mentioned here is conclusive, and no detailed ecological study of the coati in the tropical forest can be completed until an adequate study is made of the litter fauna. Ideally, such a study should be continued for several consecutive years and should include samples of the upper layers of the soil as well as the litter, since coatis dig for much of their food.

Large scale excavations are made to capture tarantulas, crabs, lizards, and mice that take refuge in burrows (pl. 12). I have seen coatis spend up to forty minutes on such excavations, partly or wholly disappearing from view as the tunnel grew longer. Usually, however, the job is completed in ten minutes or less.

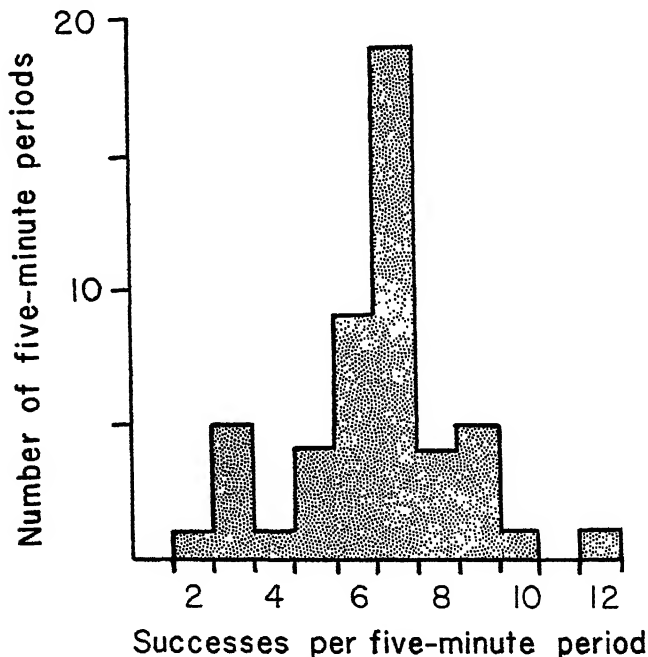


Fig. 18. Number of observation periods in which given numbers of animals were eaten. Observations were made for periods of 5 or more consecutive minutes; each litter animal eaten was counted as one success. For example, in 19 of the 51 five-minute periods, 7 animals were eaten.

Whatever the depth of the hole, from less than an inch to three feet or more, the technique of digging is the same. Both front feet are used alternately and rapidly while the dirt showers out behind. Every few seconds the paws are withdrawn and the snout is thrust as far as possible into the hole. The digger frequently backs out of large excavations to look around, and on these occasions may drag out some of the loose dirt accumulating in the hole. The loose material dug out is also investigated with the nose. But I have never seen a coati dig with its snout—all of the actual digging is done with the strong-clawed front feet. Published statements attributing the small pits dug by coatis to hoglike rooting are apparently the result of careless observation or assumption.

Occasionally the digging is in vain, but if it is prolonged one can be reasonably sure that the coati knows the location of the prey and will eventually come up with it. The imminent capture of a vertebrate or large invertebrate is signaled by an increase in the tempo of the digging and sniffing, accompanied by various grunts and squeaks.

Adult coatis seem to be the most persistent diggers. One lizard was chased into a burrow by a juvenile female, who followed it in past her shoulders, and backed out with the lizard in her jaws. She carried it off a few yards to eat it, but soon the lizard came racing back, minus its tail. This time it took refuge in a deeper hole, but was seen by the young coati's mother, who set about digging it out. The juvenile ate the wildly flopping tail, then came over to see about the rest of "her" lizard. She was chased off, however, and soon gave up. The adult female dug for ten minutes before she was able to reach and kill the lizard. Two other females—an adult and a subadult—chased a lizard down a burrow at the base of a tree. Both sniffed around excitedly and began digging. But after ten minutes the younger animal gave up, and the adult dug alone for thirty minutes more before she made the kill. Besides several smaller holes, which the younger female helped to dig, she dug an excavation three feet long, by one foot wide, by one foot deep. Digging was greatly hampered by the network of tree roots and several of these were bitten through, or grasped in the teeth and pulled until they broke. Another adult female dug a lizard from a burrow in twenty minutes, completely disappearing into her excavation, which extended more than three feet into the hillside. Chapman (1938) saw an adult male coati dig a tarantula out of loose fill in the clearing; a hole thirty-two inches deep by fourteen inches wide at the mouth was completed in five minutes.

Crabs are dug from shallow holes in stream beds or trapped in pools. One female that had just captured and eaten two crabs in a stream in which she was prowling, moved into a small pool and "dredged" the bottom. She moved her paws straight forward and back in parallel, alternate motions that seemed very mechanical in contrast to the fidgety movements of a raccoon as it explores the bottom of a pool in all directions. Band 1 was the only band whose home range boundaries included part of the lake shore. Although they went near the shore on their travels occasionally, they never foraged there or took any particular notice of it.

Stumps and fallen logs receive close attention from foraging coatis (pl. 13). Often crabs are caught under logs or stumps, and I once saw a mouse run out unnoticed from under a log that was being swarmed over by a band of very excited

coatis. More often the yield is millipedes and insects. The bark is ripped off, and if the wood is well decayed the whole log may be ripped apart by the powerful forepaws, with pauses while the ever-useful snout sorts through the debris. Blow-downs, with their tangles of logs, brush, and low plants, are favorite foraging places. Dead stubs are climbed and searched from top to bottom (pl. 14). I once saw three subadults nearly demolish a rotten twelve-foot stub which they all climbed and attacked simultaneously, ripping off large pieces with their forepaws as they clug to the diminishing support.

Many insects are captured above the ground in low plants and hanging debris. Patches of piñuela (*Ananas magdalenae*) are favorite hunting grounds and are worked over carefully. All parts of the plant above ground are investigated. The coatis rear up on their hind legs to examine the long narrow leaves for insects hiding in the creases where the leaves are bent down (pl. 15). They also pull back the leaves to examine their bases, and dig in the fleshy base of the plant.

A clump of small palms is similarly investigated, the coatis sniffing and digging at the base, rearing up on their hind legs, climbing up into the clump, or jumping up and pulling down individual fronds. Rotting palm fronds and clusters of dead leaves and moss in low bushes are pulled apart with the front paws, and the insects in them are snapped up with the teeth. Frequently large flying insects are found in such places, and these are pursued to their landing place if they escape the initial grab. One female reared up and batted at a hanging stick, then grabbed it in both paws, bit off a piece, examined it, and tried another piece before she found what she had smelled there.

Six times I saw foraging coatis ascend living trees to hunt for food in the rotten wood in large cavities.

KILLING METHODS

Several methods are used by coatis for killing their varied prey. Perhaps the most distinctive is the habit of "rolling" certain small animals under the front feet, as discussed by Ingles (1957). The victim is pulled into the open and rolled rapidly under the thick pads of both forepaws in an alternating back-and-forth motion. The "dredging" movements of the female in the stream pool were a slow-motion version of this action, just as the raccoon "dredging" is similar to the nervous rolling of small objects by raccoons. (Raccoons also use these rolling movements to kill small arthropods and fish.) Rolling is usually continued until after the animal is dead and well mangled. This method of dealing with the prey presumably serves two functions: the killing of animals that have harmful bites or stings with a minimum chance of being hurt by them, and the removing of various hairs, bristles, and chitinous structures that make some invertebrates difficult or unpleasant to eat. Most of the animals rolled have these characteristics: small crabs, arachnids, bristly caterpillars, stinging insects such as wasps, and beetles and other insects with spiny projections on the exoskeleton. There are no hard and fast rules as to what should be rolled, and young coatis tend to roll a greater variety of animals than do adults. Vertebrates are usually not rolled, but I saw an adult female make rolling motions on the upturned belly of a large frog she had just killed, even though the frog did not roll and the skin was not broken. A juve-

nile that had been isolated from other coatis before her eyes opened rolled mice that were fed to her several months later. She had never fed on live food, and the rolling was rather clumsy. A wild juvenile in one of the bands pounced on a scorpion and rolled it under her paws, but she stopped and bit at it before it was dead. She was stung on her right forepaw and on her mouth, but chewed and swallowed the scorpion and merely shook her paw and scratched at her snout a couple of times. Although the rolling response is present in coatis that have never seen the action performed, it seems less efficient in inexperienced coatis. Both the technique and the choice of objects to be rolled are refined with experience.

Although tarantulas are invariably rolled, land crabs are usually dealt with differently. Experienced coatis first drag or maneuver the crab into the open, and then usually pin the chelae with the forepaws and bite through the front of the carapace. The claws may be bitten off immediately (even before the crab is killed), or left until last. I watched an adult female handle a crab that had backed into a small niche under a log and was defending itself well in these close quarters by waving its chelae back and forth in the coati's face. She began by digging out the dirt under the log, getting more room in which to maneuver. Then she dislodged the crab from its refuge with a quick motion of her paws. Once she had the crab in the open, she quickly pounced on it and bit off its claws.

The coati typically pins vertebrates with its forepaws, and the kill is made cleanly by a quick bite through the skull. This is not so simple with a caecilian since the head is so small and poorly defined. These animals are bitten several times (just as likely on the hind end as on the front) and then are eaten, starting at one end. If the hind end is chosen, the animal may remain alive for some time. Lizards and mice present no problem, and once pinned by the paws are quickly killed by a bite through the head. Several large spiny rats (*Proechimys semispinosus*) that were given to captive coatis caused more trouble, however. Care was required in biting the head to avoid the rat's teeth, and several bites were required for the kill. Inexperienced coatis showed poor technique, failing to pin the rat effectively, biting indiscriminately at any part of the body and having tug-of-war bouts with other coatis with the still-living prey.

EATING METHODS

Different foods are also eaten in different ways. Most small invertebrates are chewed whole just as they are picked up. Small animals that are rolled are also picked up in the teeth and eaten whole. The carapace of a crab is opened with the front paws and teeth, and the contents are licked out. Some pieces are chewed up, shell and all. Large insects, tarantulas, and vertebrates are manipulated with the forepaws so that the head is pointed up, and this is usually eaten first. Then the bites progress posteriorly. With insects, small lizards, and mice this is a fairly tidy process. Caecilians, being so thin and rubbery, are hard to manipulate and to bite into pieces. The usual solution is to hold one end down with the forepaws and pull up on the other end with the teeth until a piece comes off, when the rest snaps back like a rubber band. With larger vertebrates, the process is not very regular. Often, after biting the head for the kill, all or part of the head is eaten; but then the belly and/or chest cavity may be split open with the forepaws and teeth, and the

Family	Species	Common name	Part of plant eaten
Palmae	<i>Astrocaryum Standleyum</i> Bailey <i>Scheelea zonensis</i> Bailey	black palm	Orange pulp surrounding nut. Thin yellowish pulp between tough outer covering and nut.
Bromeliaceae	<i>Ananas magdalenae</i> (Andre) Standl.	piñuela, wild pineapple	Succulent leaf bases, may eat fruit.
Musaceae	<i>Musa sapientum</i> L.	banana	Fruit (cultivated in clearing).
Moraceae	<i>Cecropia mexicana</i> Hemsl. <i>Ficus</i> spp. fig	Dry pistillate spikes, 12-20 cm long. Pulpy fruits of several species, up to 4 cm in diameter.
Annonaceae	<i>Annona acuminata</i> Safford	Dry fruit, up to 2.5 cm in diameter.
Leguminosae	<i>Dipteryx panamensis</i> (Pittier) Hubbard and Rehder	almendro	Only thin greenish outer covering of the large elipsoid seeds, up to 6 cm long.
Anacardiaceae	<i>Anacardium excelsum</i> (Bert. and Balb.) Skeels <i>Mangifera indica</i> L. <i>Spondias Mombin</i> L.	espavé mango hogplum	Nut. Large fruit with thick, stringy pulp, escaped from cultivation. Pulp of fruits (yellow, juicy drupes, similar to plum in appearance).
Sapindaceae	<i>Cupania fulvida</i> Triana and Planch	Seeds from three-parted capsule.
Tiliaceae	<i>Apeiba aspera</i> Aubl.	monkey-comb	Small seeds from dry, sea urchin-like pod.
Caricaceae	<i>Carica Papaya</i> L.	papaya	Large fruit (cultivated in clearing).
Myrtaceae	<i>Psidium Guajana</i> L.	guava	Fruit (cultivated in clearing).
Melastomaceae	<i>Miconia argentea</i> (Swartz) DC.	Small dry berries on panicles.
Rubiaceae	<i>Coussarea impetiolaris</i> Donn. Smith	Small white drupes on panicles.
Sapotaceae	<i>Calocarpum mammosum</i> (L.) Pierre <i>Chrysophyllum panamense</i> Pittier	mamey	Large pulpy fruits, up to 20 cm long. (Name taken from Standley, 1928.) Pulpy fruits about 2 cm in diameter.

contents eaten. The large *Leptodactylus* frog I saw eaten had its tongue and mouth lining eaten first, and then progressively more posterior portions. The spiny rats usually had their body cavities slit open early in the eating process. Toward the end of such meals, as various parts became detached, the pattern broke down. Every part of small animals, including small vertebrates, was usually eaten; but pieces of skin and bone were often left from the rats.

Although I have never seen coatis do this in the field, captives sometimes carry pieces of food in their teeth to the water pan, drop them in, and stir them around with a forepaw. This is a well-known habit of *Procyon*; however, the raccoons actively manipulate such objects in their dexterous fingers instead of just stirring them around as do coatis. Clean food is just as likely to be "washed" as is food that is covered with dirt or trash.

Coatis do not voluntarily share food, nor do they store it. All of their food is eaten where it is found or caught, except when an individual carries a particularly choice item (e.g., a small vertebrate or land crab) a short distance from the rest of the band to avoid sharing it.

PLANT FOODS

While on Barro Colorado I observed coatis eating from all of the plants listed in the table on page 190 (scientific names from Standley, 1933). I am indebted to Dr. John Ebinger, then a graduate student in botany at Yale University, for identifying some of the plants.

This is by no means an exhaustive list of the fruits eaten by coatis on Barro Colorado, since many species that might be eaten do not occur in the ranges of the coatis I followed, and some of those that do occur were not in fruit. Some that were in fruit only one year of the two (black palm, almendro) were probably the single most important items in the coatis' diet while they were available.

Only the fruits were eaten from these plants, except for *Ananas magdalenae*. The piñuela did not fruit during the course of this study but on three occasions coatis were seen to pull up or knock over small plants with their paws, exposing the succulent white leaf bases, which were bitten off and eaten.

The several species of wild figs (*Ficus*) were collectively the most important fruits in the coatis' diet. Some of them were available in almost every month, the fruit crops were very large, and the trees are widely distributed. The almendros are also widely distributed and produce large, long-lasting fruit crops. When almendros were available, the coatis in Band 4 adapted their whole pattern of daily movements to take advantage of each tree as it came into fruit. This species, however, produces significant crops of fruit only every other year, and none was available to Bands 1 and 3 during the 1959 dry season. The abundant black palms also bear prolific crops of fruit that were used heavily by Band 4 in 1960, but were not available the previous year. *Scheelea* palms provided food for all three bands, though the fruits were not so attractive as the pulpier ones of the black palm. There were large crops of hogplums both years, and they were visited frequently during the fruiting season by the bands in the Donato 3-Barbour 3 area, where these trees are concentrated. While the almendros were still available, Band 4 also ate large amounts of *Chrysophyllum* fruits; these trees were all located within the band's

SEASONAL USE OF FRUITS BY COATIS ON BARRO COLORADO

(B1 = Band 1, September 1958-June 1960; B3 = Band 3, September 1958-April 1959; B4 = Band 4, November 1959-June 1960; X = other bands and solitary males.)

[illegible]

core area. *Miconia* fruits are small and dry, but the trees are widely distributed and were carefully picked over. The dry fruit spikes of the *Cecropia* trees near the clearing were also favorites of the coatis and were available in large quantities for several months.

Coussarea is a small tree with small fruits and a limited fruiting season, but this was the only fruit available to Band 1 in the latter part of the wet season. Mangos are cultivated trees found where settlements once existed. Although none was in the home ranges of the bands I followed, several trees in other parts of the island bore heavy fruit crops and were much visited by the coatis living there. The other trees listed (*Anacardium*, *Annona*, *Apeiba*, *Cupania*, *Calocarpum*) were of minor importance: either they were not common or did not produce much fruit, or the fruit was not very attractive to the coatis.

SEASONAL USE OF FRUITS

Table 13 summarizes the seasonal use of fruit by the coatis. The dry season is the principal fruit season, and 87 per cent of all arboreal feeding occurred then. This amounted to only from 5 to 7 per cent of the total active time during the season, but more time was spent eating fruit on the ground than in trees. Some arboreal feeding went on at all hours of the day, but there was a large peak of arboreal feeding from 0600 to 0800 and a smaller peak from 1600 to 1800. The morning and evening peaks are partly due to the fact that roost trees were often adjacent to fruit trees, and the coatis fed before descending and after ascending.

Figures 19 and 20 show the location of the principal fruit trees that bore crops in the combined ranges of Bands 1 and 3 (1958-1959), and that of Band 4 (1959-1960). Crops of *Spondias*, *Cupania*, and *Ficus* fruit were apparently responsible for Band 1's temporary wanderings into the southern extremity of its home range, and *Ficus* crops were what drew Band 3 temporarily to the areas near Donato 3 and Shannon 4. Almost all of Band 4's travels outside of the core area took place in the almendro season, to the almendros in the western and southeastern parts of their home range (see fig. 13).

FRUIT-GATHERING METHODS

Fruits of most species are eaten both from the tree and on the ground. Often part of a band will feed aloft while the other members feed on fallen fruit. Juveniles especially tend to stay on the ground if the trees are large, picking up the partly eaten fruits dropped by the older animals as they move from branch to branch. Toward the end of their first year, however, the juveniles show no hesitation in making long climbs for fruit.

The only fruits I saw eaten exclusively from the ground were those of the black palm (a small tree whose trunk is densely covered with sharp spines several inches long) and *Apeiba*. The dry pods of the latter were opened only rarely in passing and were apparently not worth climbing for. *Miconia* and *Cecropia* fruits were always eaten directly from the tree.

The nuts of the *Scheelea* palm can be taken while a coati is comfortably perched on the large inflorescence or in the tree's dense crown. But the fruits of other species usually grow on the tips of slender branches and excellent balance as well as clever

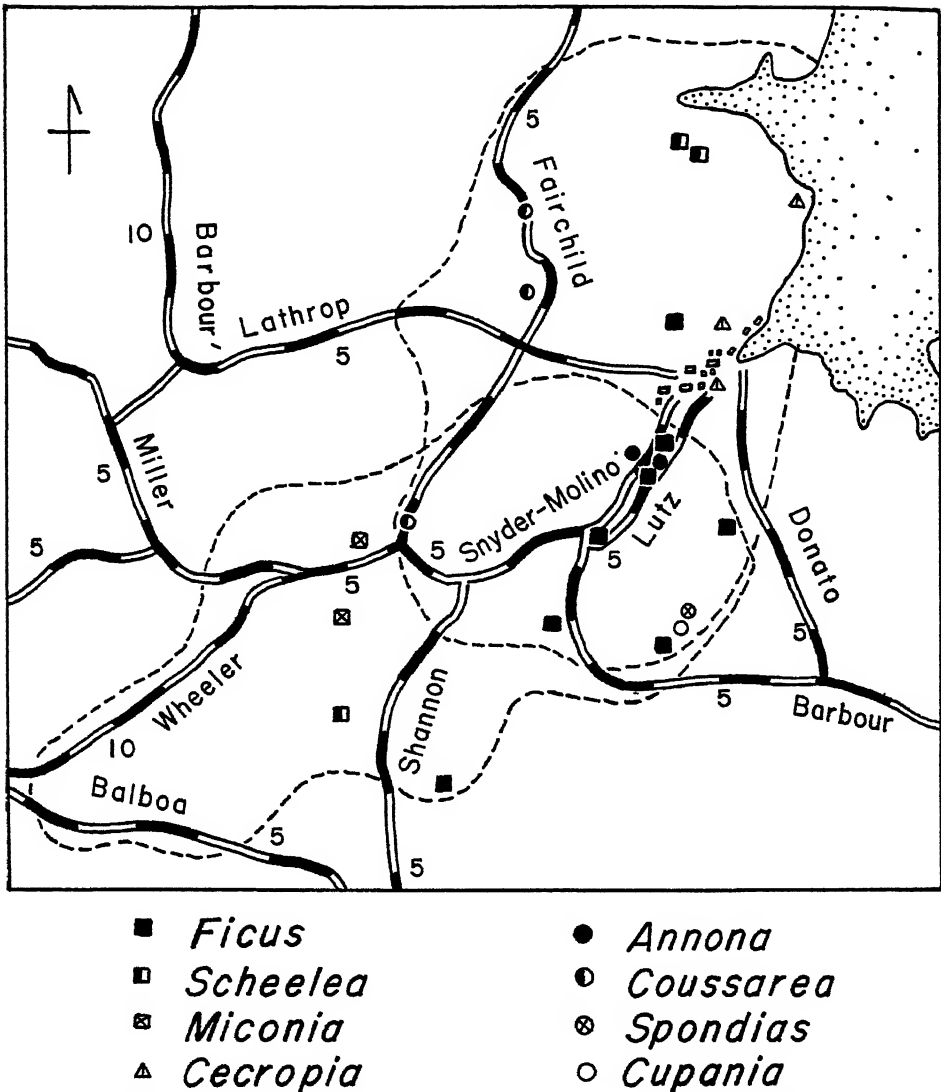


Fig. 19. Principal fruit trees which supplied food for Bands 1 and 3, September, 1958, to May, 1959. Trees which were not in fruit in this period are not shown.

footwork are required to harvest them. The coatis go right to the tip of many branches to bite off the fruits, and the tips of those too slender for adequate support are pulled in by a carefully stretched-out forepaw. The branch may then be held by both front paws while the fruit is bitten off and the coati maintains its supporting hold with the back feet. Fruit on nearby branches is also reached in this way; coatis stretch their bodies between two limbs or rear up on their hind legs to extend their upward reach. There are few fruits on any tree not accessible to the persistent coatis, which seem totally unperturbed by their precarious positions, even when a strong wind is blowing.

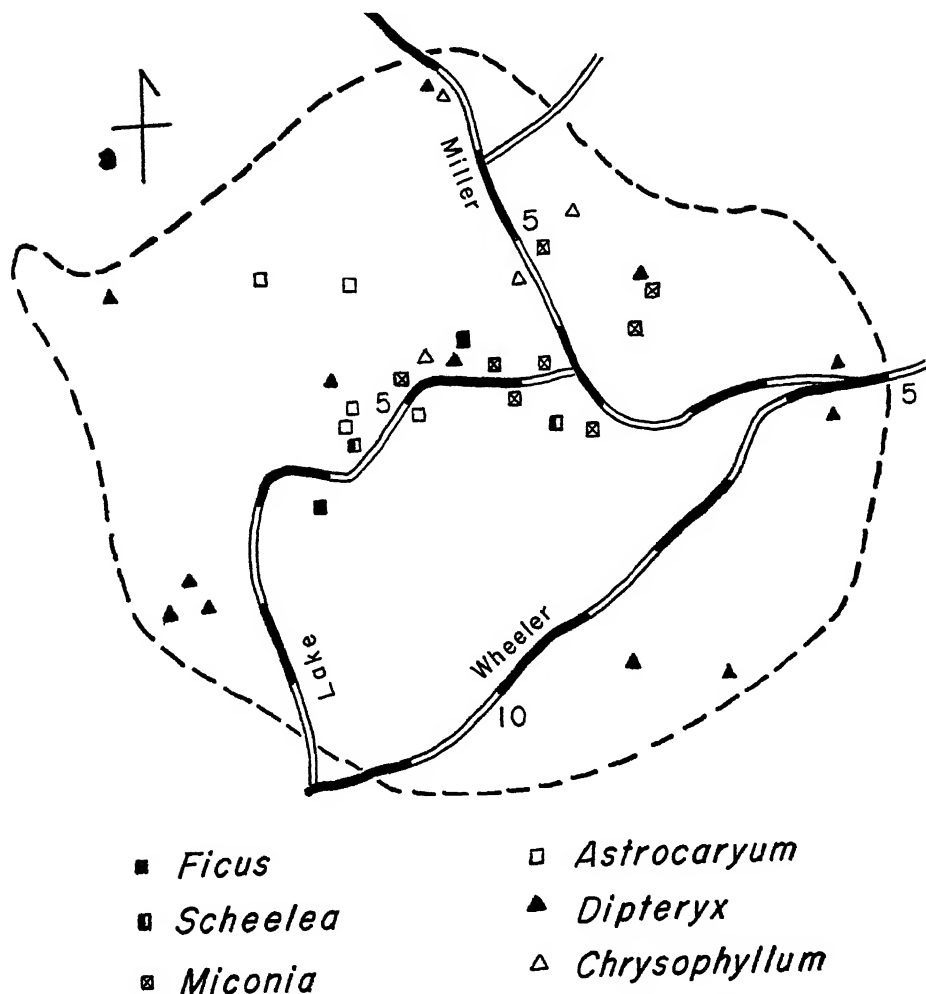


Fig. 20. Principal fruit trees which supplied food for Band 4, October, 1959, to June, 1960. Trees which were not in fruit in this period are not shown.

EATING METHODS

Although a coati's front paws are not nearly so dextrous as those of a raccoon, he makes good use of them while eating. Large fruits are ripped apart with the paws, and the pulp dug out. Frequently such fruit is eaten directly from the paws; then, if the fruit is sticky, the paws are carefully licked. Paws are also used to brush food from the lips. Banana skins are frequently opened with the snout while the fruit is held between the paws. Hard fruits such as palm nuts and almendros, of which only the outer pulp is eaten, are held between both front paws on the ground or branch while the pulp is chewed off at the side of the jaws (pl. 16).

Fruits such as hogplums are taken into the mouth whole, the pulp is chewed off,

and the seeds are spit out. Often while chewing and swallowing fruit, especially if it is soft or juicy, coatis tilt the head back and make a series of jerky gulping movements.

WATER

Free water is available in the forest at all times. When a band crosses a stream some or all members usually pause to drink (pl. 16). Even when the streams dry up there are scattered pools and innumerable small pockets of accumulated rain water. Coatis are adept at finding small puddles in cavities between the roots and buttresses of trees, in holes left where limbs have rotted off, tree crotches, woodpecker holes in fallen logs, fallen palm spadices, large fallen leaves, and hollows in rocks. Many such cavities are deep and have small surfaces for evaporation, so that water remains in them for long periods. During the wet season they are filled constantly, and often supply water during even the driest parts of the dry season. It was amusing to see a band of coatis line up to drink from a puddle, especially if it was in a tree crotch three or four feet from the ground. There was always some jostling for position on the ground and on the trunk, and occasionally the last in line found the hollow empty.

Although Band 1's home range was partly bounded by the lake there was never any need for them to drink there, and I never observed them doing so.

Coatis curl their snouts up clear of the water when drinking, and lap rapidly with the tongue in an irregular pattern punctuated with short pauses.

URINATION AND DEFECATION

The coatis displayed no tendency to deposit their scats in any particular place. Before descending from their roost trees in the morning, they usually urinated and defecated, and this was often the first indication that they were awake. During the day they dropped scats or urinated anywhere, on the ground or from the trees. The position assumed by both males and females is a partial squat with the hind legs slightly spread.

Twice I saw juveniles eating fresh scats (origin uncertain), and three times I saw adult females reingesting material they had just vomited.

LITERATURE

Published reports on coati food habits are almost as varied as they are numerous. There is general agreement that coatis eat a great variety of animals: molluscs, crabs, arachnids, insects, lizards, birds and their eggs, rodents, and carrion. And the collective published list of plant foods includes just about every conspicuous natural and cultivated fruit available where coatis are found.

It is to be expected that different items are emphasized at different times and in different habitats. Some authors, however, even though careful to describe the wide range of coati foods, have perhaps overemphasized the role of the coati as a predator on vertebrates. On Barro Colorado itself, Chapman (1929, 1938) was concerned for the future of birds nesting on or near the ground in the face of an "undisputed increase" in the numbers of coatis; and Van Tyne (1929) stated, "The nests of ant birds and other small birds are found to suffer severely from the raids of coatis..." Enders (1935) listed the coati as "a great enemy, possibly the worst"

of the small opossum *Marmosa*, and stated that in the vicinity of the laboratory clearing, where the coatis were most abundant, "How any bird or rodent survives is a constant source of wonder." These views were mostly based, however, on the enthusiasm and skill with which coatis took advantage of proffered eggs and of mammals in traps and cages. If the coatis were significantly more abundant on the island thirty years ago, their effect on vertebrates may well have been greater than it is now. But Chapman himself was unable, over a ten-year period, to detect any adverse effect on the numbers of birds owing to coati predation. He even noted that the bird for which he feared most—the tinamou (*Tinamus major*)—had increased while the coati was also gaining in numbers (Chapman, 1938).

Wallmo and Gallizioli (1954) reported alleged raids of coatis on a robin's nest, squirrels' nests, and poultry yards in Arizona, but they found only insects and wild fruits in the stomachs and scats they examined. A number of other authors (Azara, 1838; Cabrera and Yepes, 1940; Gaumer, 1917; Ingles, 1957) stressed the importance of invertebrates and fruit in the coati's diet, and the relatively small part usually played by vertebrates. The weight of good evidence supports their conclusions.

SUMMARY AND PERSPECTIVE

The food habits of coatis are of interest chiefly because of the variability and adaptability they demonstrate. The small invertebrates in the low plants and litter of the forest are the Barro Colorado coatis' chief year-round source of food, and over 95 per cent of their active hours are spent hunting for these animals. The coatis' physical adaptations fit them well for such work: highly developed olfactory equipment for locating small, unseen prey; and powerful clawed front feet for digging and ripping that prey from its strongholds in the ground and fallen logs. Coatis make little effort to search out larger prey, and vertebrates are only incidental items in their diet.

The coatis' quick reactions and formidable weapons enable them to handle larger prey readily whenever it is encountered. Under certain conditions they can become efficient predators, and individuals may develop considerable skill as hunters. But their usual pattern of noisy, unalert foraging is not an efficient one for the capture of vertebrates. Coatis have not developed the precise stalking and attack procedures that typify the hunting behavior of such specialized carnivores as the cats (Leyhausen, 1956).

Coatis are preëminent opportunists with large appetites, and they are quick to take advantage of any dietary good fortune that comes their way. Sharp, strongly curved hind claws, and an excellent sense of balance aided by their long tail adapt coatis for agile aboreal maneuvering and enable them to partake heavily of any seasonal fruit crops. For short periods these fruits may even provide the greater part of the coatis' diet.

A further demonstration of the coatis' adaptable eating habits is the alacrity and persistence with which they descend on particularly fine concentrations of food. They often center their activities not only on such natural bonanzas as large crops of figs and almendros, but on cultivated crops, orchards, and garbage piles as well. They frequent a source regularly until it is exhausted, or until a more

attractive one becomes available elsewhere. Thus the laboratory clearing on Barro Colorado, with its generous handouts, abundant fruits, large insects and tarantulas, and populations of lizards and mice displaced periodically by grass cutting and clearing operations, has long been a gathering place for coatis. Enders (1935) and Chapman (1938) both commented on the abundance of coatis in the clearing, and on their disappearance at times when large natural fruit crops became available in the forest.

The solitary males especially tend to congregate and stay in such places. The bands also take advantage of these special food sources and frequent peripheral areas of their home range to do so. But they seem to include such areas in their regular travels rather than settling down there as do some males. The bands I baited came and went with great independence, and sometimes I waited for them at food stations in vain for days or weeks; Band 1 made frequent but irregular visits to the clearing while covering the rest of its range in an apparently normal manner. In contrast, several adult males would sit for hours at a food station or outside the kitchen door, waiting for a handout. This was one reason why my data on the "natural" behavior of such males are so meager; individuals tame enough to follow usually were not inclined to move, and so we sat and watched each other.

Attempts to study coati food habits with captive animals pointed up the dangers of generalizing from the results of artificial behavior experiments. The experiments helped to clarify certain points, but much of the information gained from them was misleading. Foods that were readily eaten in the wild, including such favored prey animals as tarantulas and land crabs, were ignored in the pens. Even when tarantulas were attacked, the coatis showed little enthusiasm; the rolling process was poorly developed, and the tarantulas often survived, or if killed, were not eaten. This occurred with adult coatis that on other occasions had shown not only their liking for such prey but their skill in dealing with it. These captives were not overfed and still accepted other food readily. Semitame coatis in the clearing and even in the forest often showed a similar lack of response to proffered food items that normally they would have fought over.

Spiny rats, however, were usually attacked immediately in the pens, and the readiness of wild coatis to take small mammals from traps has already been mentioned. Alleged instances of wild and tame coatis raiding poultry yards have been noted by Wallmo and Gallizioli, 1954, and Aldrich and Bole, 1937. These cases emphasize the coatis' strong liking for vertebrates and their readiness to accept them when they are easily accessible, but should not be taken to mean that coatis normally concentrate on vertebrates.

SUMMARY

The coati (*Nasua narica*) was studied at the Smithsonian Institution's field station on Barro Colorado Island, Panama, from July, 1958, to June, 1960. Field observations of wild coatis were made throughout the island, and close contact was established with five bands. Four of these were followed intensively for periods of up to nine months each. In addition, nineteen coatis, including one entire small band, were kept in captivity for varying lengths of time, and two litters born in captivity.

Coatis are chiefly diurnal; the daylight hours are spent traveling and feeding,

and there are occasional rest periods. At night the coatis usually retire to one of a number of roost trees scattered over their home range, and sleep from approximately sunset to sunrise. However, adult males are often active at night and there is considerable nocturnal activity in the mating period.

The females, and males up to two years old, are grouped into loosely organized bands with from about four to twenty members, based on the family unit of an adult female and her young of the past two years. When the males become sexually mature at the end of their second year, they take up a solitary existence. Mutual hostility almost invariably marks the encounters between adult males, but actual fights are rare except in the mating period. Members of bands are usually hostile to adult males when they meet, attacking and driving them off, but are less hostile to members of other bands. Within a band the closest bonds are between adult females and their young of the year. There is no clearly defined dominance hierarchy, except that juveniles, due to the active support of their mothers, are generally dominant over subadults and adults. Mutual grooming between members of a band is common, but there is little cooperation of other kinds, and there is always active competition for food.

The coatis on Barro Colorado have a single annual breeding season. The mating period lasts for about one month early in the dry season. At this time an adult male typically joins each band and stays with it during the entire mating period. He is completely subordinate to the females in the band. He grooms with them and sleeps in the same roost tree on most nights; copulation takes place mostly at night. Other solitary males, especially younger males without bands of their own, often approach the bands, but they are usually resisted by the females, and are attacked and driven off by the adult male accompanying the band.

The gestation period is ten to eleven weeks, putting the time of birth near the transition from dry season to wet season. In 1959 the young were born in May and June; in 1960 the first litters were seen in mid-April. About one week before the young are born, the pregnant females individually leave the band and build tree nests. The young are born in the nests and stay there for about five weeks. During this time the females divide their time between caring for their young and foraging alone for their own food. The nonbreeders in the band apparently remain more or less together during this period, although the maturing males are becoming more independent as the time when they will leave the bands permanently approaches. When the young are able to run and climb well enough to keep up with the band they are brought to the ground and the band reunites. In 1960 this happened in early May.

The bands have undefended, overlapping home ranges; those that I measured ranged from 34 to 45 hectares. Within each home range is a core area that is used constantly throughout the year; the peripheral areas of the range are visited only intermittently except when preferred fruits are available. The core areas do not overlap, and each band spent about 80 per cent of the time that I observed it in its core area. Thus effective spacing of the population is achieved without strict territorial defense. The average of the daily minimum net movements of bands was between 1,500 and 2,000 meters; some bands traveled more than others, and all bands traveled more in the wet than in the dry season. Adult males apparently

also have home ranges, but are more inclined both to wander and to localize near particularly good food sources. Between September, 1958, and April, 1959, the population I was following closely decreased from about 30 to 15 individuals, and there was very little reproduction in 1959. Breeding was more successful in 1960, and the population increased. The fragmentary evidence available indicates that populations of tropical mammals may not be so stable as is commonly assumed.

Coatis are omnivorous. Their principal source of food is the invertebrate fauna of the forest litter. They readily chase and eat small vertebrates, but do not seem to put much effort into searching for them; vertebrates were only an incidental item in the diet of the coatis I watched. A wide variety of fruits is eaten in season, and for short periods a single species of fruit may be the main item in the diet.

The behavior of coatis in general is flexible and opportunistic, which probably accounts in large measure for their success in a wide variety of habitats.

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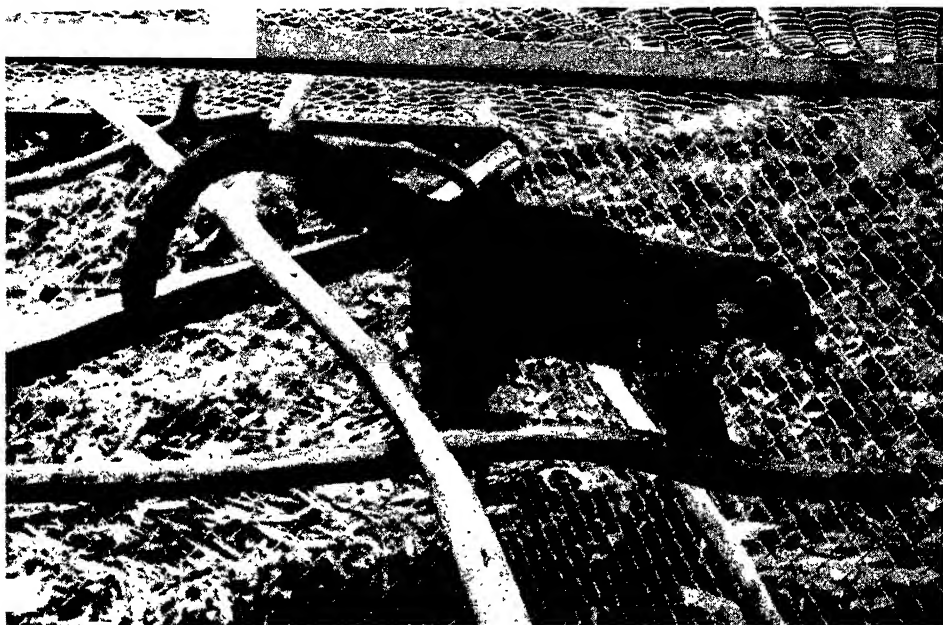
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PLATES



a. Adult male coati.



b. Adult female coati.



Typical forest floor scene showing lack of dense undergrowth



c Vines foraging among roots of *Bombacopsis Fendl* in one of the largest trees in the Barro Colorado forest



b Blow down showing dense tangle of vines pulled down by fallen tree



a Subadult male showing black mark on rump



b Pens for captive coatis Each pen is 30 by 15 by 6 feet and has a cement slab floor



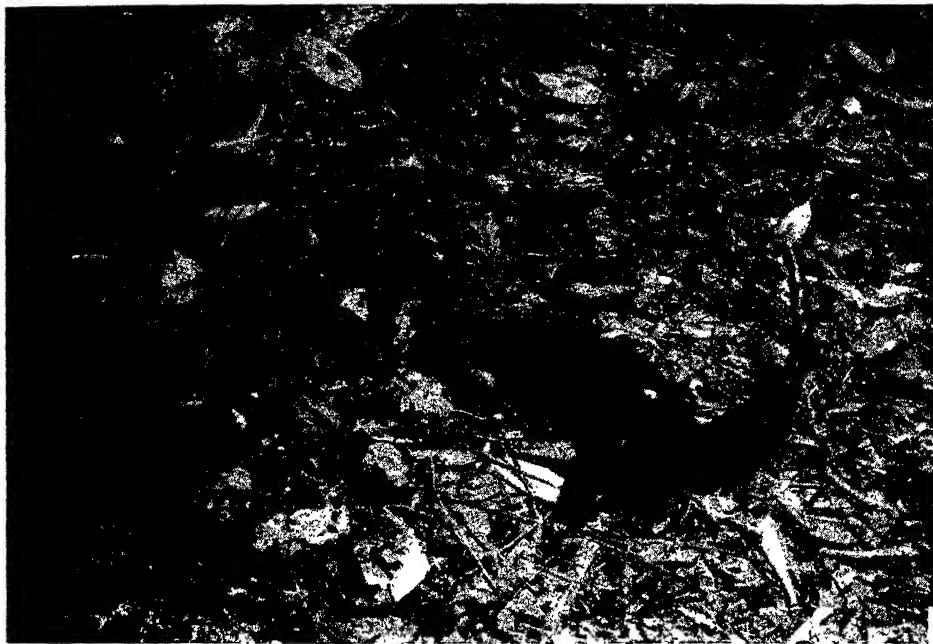
a Banisteria in daytime in tangle of lianas 25 feet above the ground



b Coati dozing on the ground in daytime



Juveniles in alarm position on tree.



a. Subadult male investigating a turtle.



b. Self-grooming with the teeth.



a. Typical scratching posture.



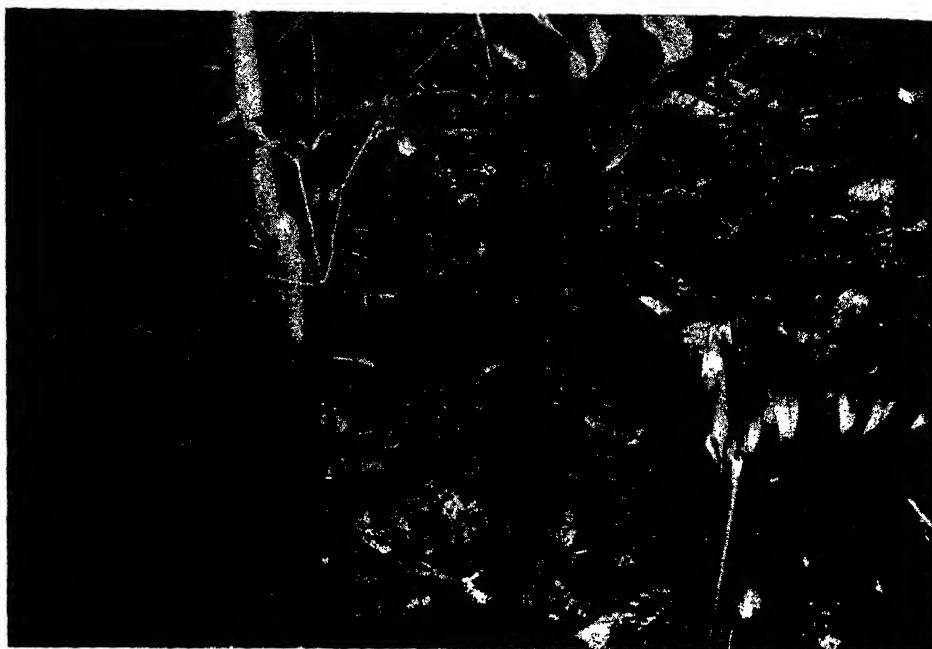
b. Typical scratching posture.



a. Band of adult females and 9-month-old young foraging (Band 4, January, 1960).



b. Adult females with their 6-week-old young (Band 4, May, 1960).



a. Typical mutual grooming positions.



b. Group grooming session between adult male (second from left), adult female (third from left), and her young, in the mating period (Band 4, January, 1960).



a. Adult male rubbing urine on liana during mating period.



b. Juveniles engaged in chasing and inhibited fighting.



a Foraging in the forest litter



b Digging out a tarantula



a Foraging in a rotten log Note destruction of log



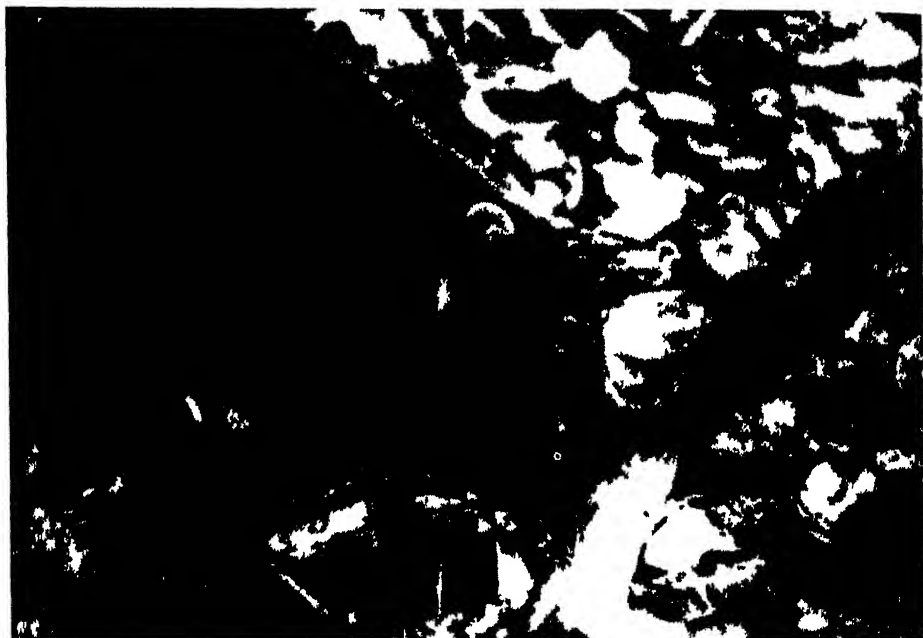
b Foraging in a stump



Foraging in a leaf-stub



Foraging in a piñuel plant



a. Chewing the pulp from an almendro nut



b. Drinking from a stream. Note turned up nose of juvenile in foreground

THE INTEGRATION OF AGONISTIC
BEHAVIOR IN THE STELLER'S JAY
CYANOCITTA STELLERI (GMELIN)

BY
JERRAM L. BROWN

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THE INTEGRATION OF AGONISTIC BEHAVIOR IN THE STELLER'S JAY, *CYANOCITTA* *STELLERI* (GMELIN)

BY

JERRAM L. BROWN

(A contribution from the Museum of Vertebrate Zoölogy of the University of California)

INTRODUCTION

PERSPECTIVE

AGGRESSIVE BEHAVIOR HAS CENTRAL IMPORTANCE in contemporary ethological theories concerned with the evolution and "motivation" of behavior. It is hoped that the work reported here will serve to give these theories a firmer foundation in fact and to lead to modifications where appropriate. At the same time the work is exploratory, in the sense that it deals with a species whose agonistic behavior has not received any significant previous study, the Steller's jay (*Cyanocitta stelleri*).

Conspicuous in most animals are behavioral responses concerned with escape, defense, and offense. These behavior patterns may be discussed collectively as agonistic behavior. The necessity for self-protection and the often opposing tendency toward aggressive intraspecific competition have placed a selective advantage upon certain patterns of agonistic behavior. In many species of birds and mammals such behavior has an important influence, not only on the lives of individuals, but also on the form of social organization characteristic of the species, which in turn is closely related to the ecology of the species. As a consequence of the important role which aggressiveness plays, complex behavior patterns have evolved; conspicuous structures have evolved in some species to supplement or reinforce those patterns. Many characteristics of birds, such as their songs, calls, displays, and coloration, are thought to have evolved in the service of agonistic behavior.

The many advantages of birds as subjects for behavior study have resulted in a large body of data on agonistic behavior in birds. It is, therefore, not surprising that the theories concerned with the motivation and evolution of avian displays observed in aggressive contexts have been prominent among recent behavioral studies. Concerning the evolution of behavior patterns, theories have been proposed that various displays, many of them hostile, have been derived from movements which initiate locomotion (Daanje, 1951), from displacement activities (Tinbergen, 1951), and from autonomic regulation of feather posture (Morris, 1956). The theoretical influence of the nature of the nesting environment on the evolution of hostile displays has also been studied (Cullen, 1957). Concerning the integration of behavior, the authors of many recent studies have theorized that hostile displays in a variety of species have, as their "motivation," characteristic states of conflict between attack and escape "drives" or "tendencies" (e.g., Tinbergen, 1959).

The problem of the integration, or "motivation," of agonistic behavior has attracted considerable attention. The Steller's jay has been especially useful for

the study of this problem, because of the complexity of its behavior patterns, the ease with which aggressive encounters could be studied in the wild in color-banded individuals, and the unusual advantages for study provided by the crest. These factors have allowed the quantitative study of certain aspects of integration which had previously been studied largely by qualitative methods.

Because comparisons with other species are useful primarily with reference to evolutionary problems, and because the focus in this paper is on the integration of agonistic behavior rather than its evolution, few such comparisons are made here. References to works on the integration of behavior are limited in the main to general theory, because species differences make comparisons of specific behavior patterns difficult to interpret. Some comparisons have been made, however, with the European jay (*Garrulus glandarius*), since it was the only other jay for which detailed published descriptions of behavior were available when this paper was written.

AN APPROACH TO BASIC PROBLEMS

The basic problems of the study of animal behavior may be classified under: (1) the evolution of behavior patterns and abilities; and (2) the integration of behavior (including its ontogeny).

In this paper the term "integration of behavior" will be used in the sense of the processes which coordinate effector actions into behavior patterns. The determination of which effector processes or combinations of them are to be activated or inhibited in any situation depends primarily upon two groups of factors: (1) the physical and chemical phenomena which constitute the impinging external and internal stimuli to the receptors; and (2) the biological phenomena which constitute the integrative mechanisms of the individual. Among the more complex integrative mechanisms of behavior are the phenomena that have been loosely referred to as motivation. This paper is concerned primarily with those integrating mechanisms which might be classed as the motivation of agonistic behavior.

When exploring the integrative mechanisms which intercede between receptors and effectors, the inquirer should consider the central nervous processes, even in a purely behavioral study. Because changes in the environmental stimuli eliciting agonistic behavior are relatively easily observable and generally known, and because they exert their influences on behavior through the central nervous system (CNS), the problems in the study of the integration of agonistic behavior focus on the neural mechanisms which are inevitably involved. In order ultimately to understand the integrative processes of behavior it would be desirable to know the spatial and temporal patterns of activation and inhibition throughout the nervous system which accompany and determine, or "motivate," each behavioral act. I believe that more progress can be made in this field by setting up physiological hypotheses that recognize the fundamental role of the CNS and incorporate both behavioral and physiological information than by restricting the interpretation of behavioral observations to purely behavioristic correlations. Only by explicit recognition of the processes of the nervous system can the integration of any behavior be understood.

Considerations of purely behavioral observations cannot alone reveal how the CNS integrates behavior. However, changes in behavior generally involve changed neural states, and so a basis exists for inferring changes in neural activity from observed changes in behavior—with appropriate precautions and qualifications, of course. It is this very correspondence between behavior and neural activity which allows the behavioral study of "motivation." When behavioral observations may be organized into meaningful patterns capable of being confirmed by other investigators, properties of the CNS responsible for the integration of these patterns may be postulated, and the investigation of these patterns may proceed further. Such studies result in theories which are more amenable to testing by neurophysiological methods. Therefore, the basic assumption of the behavioral approach to the problem of the integration of behavior is that useful information concerning the integration of behavior by the CNS may be derived from strictly behavioral observations, provided their interpretation is cognizant of physiological knowledge.

Although any single observation of behavior in a bird supplies some information concerning activity which has occurred in the CNS, the investigator may, by combining various types of concurrent observations, especially in a quantitative manner, state much more accurately his hypotheses predicated certain coordinative properties of the CNS for particular types of behavior and thus make his theories more susceptible to further testing behaviorally and physiologically. Therefore, the behavioral observations, and especially those concerning crest elevation and associated behavior, will be considered here in respect to the information which they contribute to our understanding of integrative properties of the CNS for aggressive behavior.

The principal method by which observations of behavior in the field and in the laboratory have contributed to our understanding of the integration of behavior has been as follows. When the functional type of behavior (such as feeding, avoidance, aggression, etc.) remained the same but its intensity or frequency increased, it has been assumed that the populations of neurons responsible for the type of behavior in question were more active (firing more frequently as a population). Such a point of view was explicitly stated by the psychologist Steller (1960:1509), when he expressed the following working assumption: "From a physiological point of view, drive, whatever its origin, must be equivalent to the degree of activation or arousal of the excitatory neural mechanism operating in motivation." Using implanted electrodes, similar increases in intensity in a given type of behavior have been obtained by increasing the intensity or duration of electrical stimulation (von Holst, 1957; de Molina and Hunsperger, 1959). These experiments support the validity of the assumption to a considerable extent. In the wild animal, however, the decision whether certain behavior patterns are to be interpreted as due to activation of one pool of neurons or of two or more such pools may become arbitrary. Furthermore, it would be naïve to think that complex behavior sequences are integrated by only one population of neurons (Hinde, 1959).

It is necessary to distinguish clearly between (1) empirical observations of behavior and (2) theoretical inferences concerning integrating mechanisms (e.g.,

territorial boundaries was characteristic of Steller's jays but not of scrub jays; however, neither species conspicuously avoided territories occupied by the other species.

The habitat of Steller's jays in western North America roughly coincides with coniferous forests in the Transition and Canadian zones, but in the Berkeley region and elsewhere in coastal California the species occurs in broad-sclerophyll forest and areas where groves of eucalyptus trees occur adjacent to such forest. The jays in the study area made heavy use of acorns in their diet, but this is not typical for the species as a whole.

Steller's jays in this region were typically paired and on their territories at all seasons. No migration was detectable, and changing of mates was rare. Local dispersal of the fall population seemed to be accomplished by first-year birds. Courtship typically began in March or April. After several days of displaying (special displays designated here as Sexual Sidling and Circling¹) by the male, courtship feeding of the female by the male became common, and continued through the period of incubation and brooding. Young were raised in May and June and were fed by parents into July. Molt occurred from June through September. Seasonal changes in sexual and aggressive activities roughly paralleled the seasonal changes in relative frequency of vocalizations shown in figure 1. Courtship and nesting activities occasionally occurred on warm fall days. But no completed nests were found at that season.

Although territories and territorial behavior will be referred to, the Steller's jay was not conspicuously territorial in the currently accepted meaning of the term. There was an area, centered on the nest, within which each paired male jay was dominant to all other jays all year. In the same area his female was dominant to all other females. As the distance from this area increased, the number of jays subordinate to him decreased and the number dominant to him increased. Ideally, therefore, the dominance relations of any territorial male or female with other jays in the population may be regarded as a series of concentric zones of decreasing dominance as the distance from the nest area increases. The overlapping of each individual's zones with the zones of other members of the population resulted in a complex dominance structure within the population such that dominance hierarchies recorded at any two points not far apart usually differed in the relative status of at least a few jays and were never, or only rarely, dissociated from the local environment context (Brown, 1963).

Within an hour it was often possible to observe aggressive encounters among ten or more individuals at certain locations. The fact that from such observations it was possible to construct dominance hierarchies for almost any location in the study area at all times of year shows that territory defense was not complete, and that jays commonly ranged into neighboring, and even distant, territories.

Defense of the area very close to an active nest was conspicuous. Defense of the area of dominance occurred, but unpredictably. The same intruding individual might be attacked at some times and ignored at others, even during nesting. Such attacks were most frequent during the prenesting phase, but even then were not completely predictable. In contrast, territorial defense in the scrub jay was much

¹ See note 4 below.

more thorough, and neighbors rarely entered another jay's territory in the breeding season, although flocks of unpaired and young jays did so in the fall and winter.

In the 63 acres of the study area, in 1960, there were 12 nesting pairs of Steller's jays (19 pairs per 100 acres) and 2 pairs of scrub jays. All of these Steller's jays could be seen at certain centrally located sources of food, and occasionally others would be present also. The distances between nests of adjacent pairs ranged from 280 feet to 550 feet.

Perhaps as a result of the fact that the dominance relationships in Steller's jay populations were complex and were continually undergoing readjustment, whereas the dominance relationships in the scrub jay were much simpler, the vocabulary of the Steller's jay, used principally in aggressive encounters, was more extensive than that of the scrub jay. Displays were also much more frequent in the Steller's jay. The two principal displays were Wing-spreading at low levels of arousal and Aggressive Sidling at high levels, but various other movements and positions of the crest, tail, wings, and body were also employed. The two principal displays, various other positions and movements, and the eleven vocalizations which are here formally recognized¹ are listed in the Contents and are discussed separately in the text.

STUDY AREA

Observations of the behavior of Steller's jays were made in Tilden Regional Park, Alameda and Contra Costa counties, California. The population of jays inhabiting the Indian Camp picnic area was chosen for concentrated study because of the relatively high population density there, and because these jays were tolerant of unusually close approach by man. The area was heavily used by picnickers on weekends from April through October, and school children in busloads visited the area almost daily in dry weather during the school year. Therefore, the jays in this area were accustomed to the presence of people and to the habit of gleaning scraps of food from picnic tables and garbage cans. It seems doubtful that the scraps left by picnickers served to increase the resident population density, because scraps were minimal during the winter and early spring when normal foods were least available to jays. It can hardly be questioned, however, that continual exposure to human beings was important in making possible the striking tameness of many of these birds. Because field work was conducted primarily early in the morning and in the colder months, human disturbances were minimal while the birds were being observed.

All generalizations in this paper apply only to the population at Indian Camp, unless I have specifically stated otherwise.

The picnic area is shaded by an open stand of tall eucalyptus trees (*Eucalyptus* spp.). On the southwest side of the picnic area rises a steep hill densely covered with blocks of coast live oak (*Quercus agrifolia*) interspersed with patches of chaparral. Along the northeast side flows Wildcat Creek, which is bordered by large live oaks and California laurels (*Umbellularia californica*). Eastward, beyond the creek, lies an extensive and dense stand of eucalyptus. The jays of this population nested almost invariably high in eucalyptus trees, but at the same time

¹ See note 4 below.

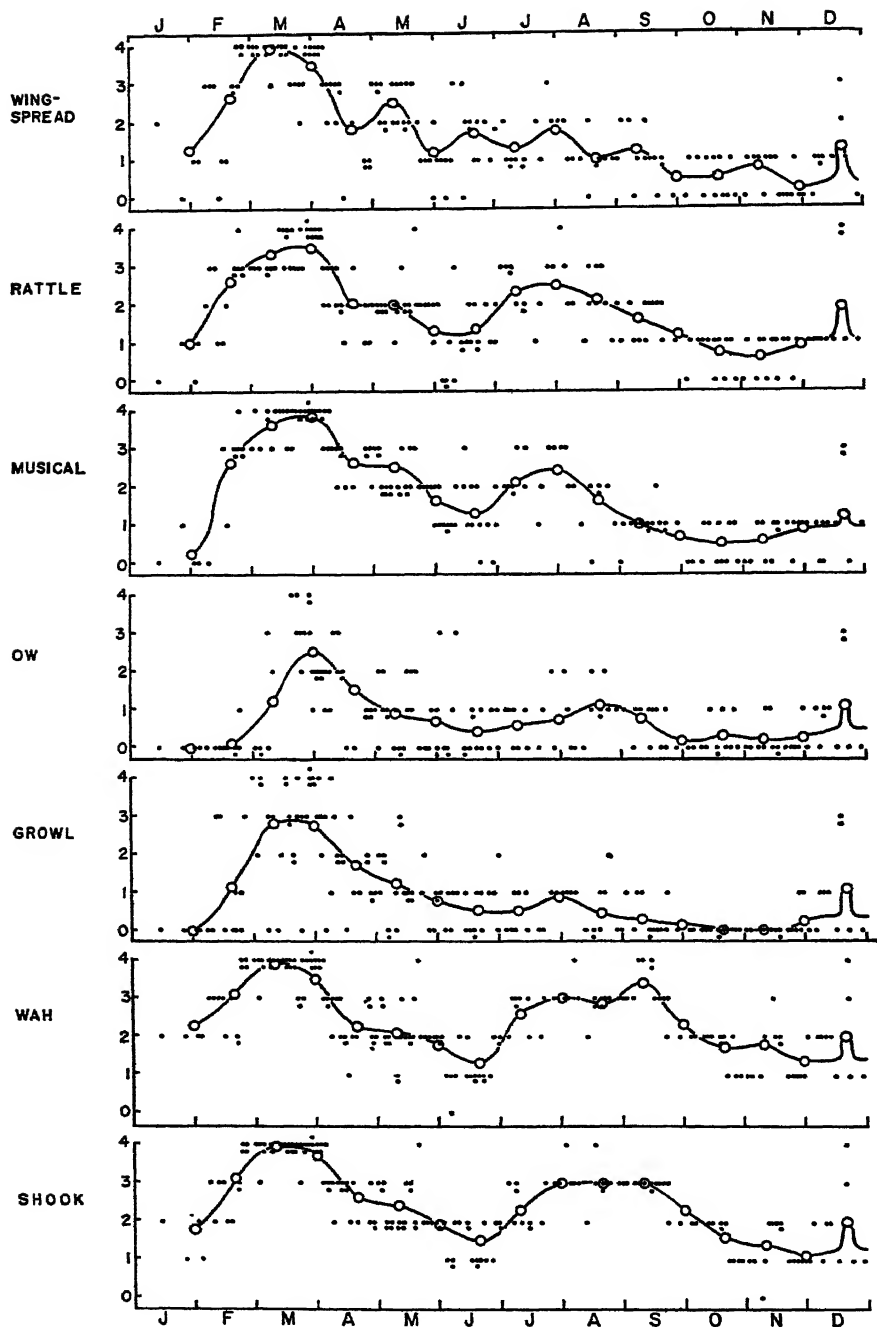


Fig. 1. Seasonal variation in frequency of Wing-spreading and six calls in a population of Steller's jays in the year 1959. Each dot represents a period of two hours or longer at comparable times in the morning in the Indian Camp study area. At the end of each period in the study area the frequencies of the various behavior patterns were scored on a relative scale, as follows: 0, absent; 1, present but rare; 2, moderately common; 3, common; 4, abundant. The trend lines were plotted from the average scores for successive twenty-day periods, which are represented by open circles. Compare table 12.

close to an area of oaks or laurels. The mosaic of vegetation types and the creek thus provided them with a variety of ecological requirements. The jays utilized the eucalyptus for nest sites; the oaks, laurels, and small grassy areas for foraging; and the creek for mud, other nesting materials, and water.

OBSERVATIONS

Field observations were made all through the year. Their seasonal distribution is indicated in figure 1, which shows that they were made more frequently during the early part of the breeding season. Observations were made for periods of two to four hours in the morning, when the jays were most active. In the period from March, 1957, through April, 1960, observations were made on 316 days and totaled approximately 730 hours in the study area.

METHODS

BANDING

From May, 1957, until September, 1959, birds were trapped on picnic tables, sunflower seeds being used as bait; and a few were caught in a mist net while they were mobbing an owl skin. Each jay was given a numbered metal band and a distinctive combination of colored plastic bands which made individual recognition possible.

In all, 114 Steller's jays were banded at Indian Camp. Of the 54 birds banded in their first year, only 9 were seen in the study area much later than the date of banding; and in only 1 of these was any breeding activity observed in its first year. Of the 58 birds banded as adults, 28 were present in the breeding season of 1960, and, in addition, others were regularly observed in 1959. Since it proved impractical to observe young or unpaired birds as they reached maturity, the observations were made almost exclusively on previously paired adults.

In 1960, 11 pairs in which both members were banded and 6 pairs in which only one member was banded were located. In 1959, the numbers were 9 and 2 respectively; and in 1958, 2 and 4. In 1959 and 1960, it was uncommon to see unbanded jays in the study area during the breeding season, and those that were seen could usually be recognized as the mates of banded individuals who nested at the periphery of the study area.

SEX AND AGE DETERMINATION

The morphological character found most useful in sexing jays was the presence of an incubation patch. Behavioral characters were found to be more useful than morphological ones, and quite reliable, especially when two or more were combined. The only jays of uncertain sex were almost invariably birds which were rarely or never observed again after being banded; consequently, sex determination was not an important problem.

Females could be recognized by the Rattle and *Ow*^{*} calls, by their passive role in courtship, by their role as recipient in courtship feeding, and by their exclusive role in incubation. Males could be recognized by the Musical and *Too-leet* calls, and by their active role in courtship and in courtship feeding. Evidence substantiating the use of these behavioral characters for sex identification will be given

^{*} See note 4 below.

later. Only the most reliable and useful characters for sexing are listed above. There are many other physical and behavioral differences between the sexes which are strongly suggestive and usually reliable, and which, though not mentioned here, may serve to corroborate sex determinations, especially when made on the bases of few observations. A summary of some differences between the sexes is found in tables 1 and 2.

TABLE 1
CRITERIA FOR DETERMINATION OF SEX IN COLOR-BANDED STELLER'S JAYS

Characteristic	Male	Female
Bill and body size in mated pair.....	Larger	Smaller
Incubation patch.....	Absent at all times	Present during brooding phase
Incubation.....	Not observed	Incubates
Courtship:		
Role in Circling and Sidling.	Usually active; rarely passive	Usually passive; rarely active
Role in mounting.....	Active (no exceptions seen)	Passive (no exceptions seen)
Role in courtship feeding..	Feeder (no exceptions seen)	Recipient (no exceptions seen)
Dominance:		
In mated pair, except in brooding phase.....	Dominant to mate	Subordinate to mate
In large group.....	Generally dominant to females	Generally subordinate to most males
Aggressive Sidling.....	In 90 of 95 observations	In 5 of 95 observations
Aerial chasing.....	Chaser in 23 of 27 observations	Chaser in 4 of 27 observations

NOTE: Certain vocalizations were found more useful than other criteria; the observed sex ratios for each call are shown in table 2.

The criteria used for age determination were those described by Pitelka (1958:40).

ESTIMATION OF CREST ANGLE

The elevation of the crest was estimated as the acute angle which the upper two-thirds of the anterior edge of the crest made with the long axis of the bill, as shown in figure 11. The basal part of the crest on the forehead was not included in the estimate. The anterior edge of the crest was usually straight, but if a wind was blowing it might be deflected in any direction; therefore, when the anterior edge was for any reason sufficiently curved to make the estimate questionable, the observation was not used. Although a general impression of the angle of the crest could be obtained in almost any view of the bird, it was necessary to have a lateral view at fairly close range to make an accurate estimate.

It was found practicable to estimate the crest angle in 10-degree intervals from 0 degrees to 90 degrees. The angle could be somewhat below 0 degrees and rarely greater than 90 degrees; such extremes were included in the 0-degree and 90-degree groups respectively. Along with the angle of the crest the whole aspects of the head changed; this provided other cues which made the estimate easier. For example,

the area of the side of the face appeared much smaller when the crest was down than when it was up. In addition, the outline of the back of the crest varied, making the 60-degree angle easy to recognize because it gave the face the appearance of an equilateral triangle. And the position of the apex of the crest varied from close to the back of the neck to over the base of the bill.

TABLE 2
COMPARISONS OF THE NUMBER OF OCCASIONS ON WHICH EACH SEX OF THE
STELLER'S JAY WAS OBSERVED GIVING THE PRINCIPAL CALLS

Vocalization	Number by			Per cent by Female
	Male	Female	Total	
Song.....	45	8	53	15
Guttural with Weak Wing-spread..	24	19	43	44
Rattle.....	0	107	107	100
Musical.....	125	0	125	0
Ow.....	+	21	21	100
Guttural with Strong Wing-spread...	100	22	122	18
Growl.....	36	2	38	5
Tee-ar.....	37	2	39	5
Wah.....	124	70	194	36
Shook.....	123	16	139	12
Too-leet.....	26	0	26	0

NOTE: Data were drawn from observations of crest angle during these calls. A "plus" means the call was recorded by that sex, but not within the same class of data from which these records were drawn (see text).

SONOGRAMS

Vocalizations were recorded in the field with a Magnemite 610-E tape recorder at a tape speed of 15 inches per second, using an Electrovoice 665 microphone mounted on an aluminum parabolic reflector. The tapes were played back on a Viking Model 75 recorder adapted to operate at 15 inches per second. Analyses were made with a Kay Electric Company Sonograph using the "high shape" filter and the wide band-pass setting. (See pls. 1 and 2.)

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POSTURES AND MOVEMENTS

WING-SPREADING

Wing-spreading was both the most conspicuous and most common display of the Steller's jay except for elevation of the crest and flicking of the tail. The term "Wing-spreading" will be employed here to include the display described below when accompanied by Guttural notes. Slight flicking movements of the folded wings were usually accompanied by other calls and occurred in very different contexts; they will be referred to as "Wing-flicking" and will be discussed separately. Wing-flicking and low-intensity Wing-spreading were thus superficially alike, but differed in many ways, of which the accompanying vocalization was the most convenient to use for practical separation (see subsection on Wing-flicking, below).

Although Wing-spreading resembled the begging of juveniles or subordinates for food, it was used in a much greater variety of contexts, and differed from begging both in the form of the display and in the calls associated with it (see below, under the topic of gaping and appeasement begging). Wing-spreading was commonly performed by both sexes, but it was observed more often in males than in females, as is shown in table 2 under Guttural with Weak and Strong Wing-spreading.

FORM

Wing-spreading is illustrated in figure 12. It could be performed while the jay was perched with the body at any one of a variety of angles, but was rarely observed in birds that were in the extreme horizontal crouching positions which were often used in juvenile or female soliciting. The legs were flexed normally, neither unusually extended nor retracted. In the lowest and most common level of intensity, which was most similar to Wing-flicking, the wings were lifted slightly away from the body briefly (intensity level 1). At intermediate intensities (level 2), the wings were jerked farther away from the body, in a motion that spread the primaries only partially, although not so little that the outer primaries made an angle with the horizontal of less than 45 degrees. At the highest intensities (level 3), the primaries were fully outstretched, and the outer primaries thus approached a horizontal position. The secondaries were rarely spread, even at high intensities, and the wrist usually remained fairly close to the body.

The conspicuousness of the wings in these positions was increased by outward jerks of the wing tips at a rate often faster than one per second. The wings were not generally fluttered or vibrated up and down, but were jerked in and out, folding and unfolding the flight feathers. The head and neck were not extended, but were kept in a normal position, with the bill horizontal. The tail could be flicked upward if the bird had recently landed, but afterward it was generally motionless, except for slight jerks accompanying the spreading of the wings (see table 3). The displaying bird usually faced the individual which elicited the

¹ The names formally designating certain postures, movements, behavior patterns, and vocalizations which I found to be characteristic or otherwise of particular significance in this study, are emphasized here by being capitalized. Of the calls, only those that closely approximate the sounds themselves are in italics.

display. The crest tended to be at an intermediate height (see Guttural, Weak and Strong, in fig. 8), with a mode at 20 degrees for levels 0 and 1 combined (Weak Guttural), and at 40 degrees for levels 2 and 3 combined (Strong Guttural). The means for Weak and Strong Gutturals are, respectively, 39 and 37 degrees.

TABLE 3
CORRELATIONS OF INTENSITIES OF WING-SPREADING ACCOMPANIED BY GUTTURALS
WITH TAIL-FLICKING AND TAIL-SPREADING

Intensity of tail action		Intensity of Wing-spreading				
		0	1	2	3	T
Tail flicking.....	0	37	4	7	21	69
	1	1	4	2	4	11
	2	4	3	7
	3	3	..	1	4	8
	T	45	8	10	32	95
Tail-spreading.....	0	44	3	12	28	87
	1	3	3	6
	2
	3
	T	47	3	12	31	93

NOTE: Wing-spreading was scored as follows: 0 = no movement, 1 = folded wings held 1-2 cm off the back, 2 = wing, partly spread, with outer primaries near vertical, 3 = wings spread with outer primaries near horizontal. Intensity scale is further explained under table 4.

The displaying bird in these positions drew attention by sounding a Guttural note which may be represented as *ut* at low intensities and *aap* at higher intensities. Females sometimes gave the *Ow* call in this display, which sounded like a modified Guttural note. The display was invariably accompanied by one of these calls, but the calls were not always accompanied by Wing-spreading. In intensity level 0 the call was given with no perceptible Wing-flicking or Wing-spreading. Virtually no other calls were observed during Wing-spreading. The call, the spreading of the wings, and the flicking of the tail, if any, were usually synchronized. The whole performance might be continued at varying intensity levels for up to two or three minutes, with slight changes in the bird's location.

CONTEXTS

Seasonal frequency.—Wing-spreading was observed in every month, and days on which it was not observed within a period of two hours were usually rare (fig. 1). It was most frequent in April of 1958 and in March of 1959 and 1960, and least frequent in November and December.

Identity of jays performing Wing-spreading.—At low intensities of Wing-spreading (levels 0 and 1), 44 per cent of the 43 individuals of known sex giving the Guttural notes were females (table 2). At high-intensity levels (levels 2 and 3), only 18 per cent of the 122 individuals of known sex were females. Of 258 recorded observations of Wing-spreading, almost all were of birds known to be

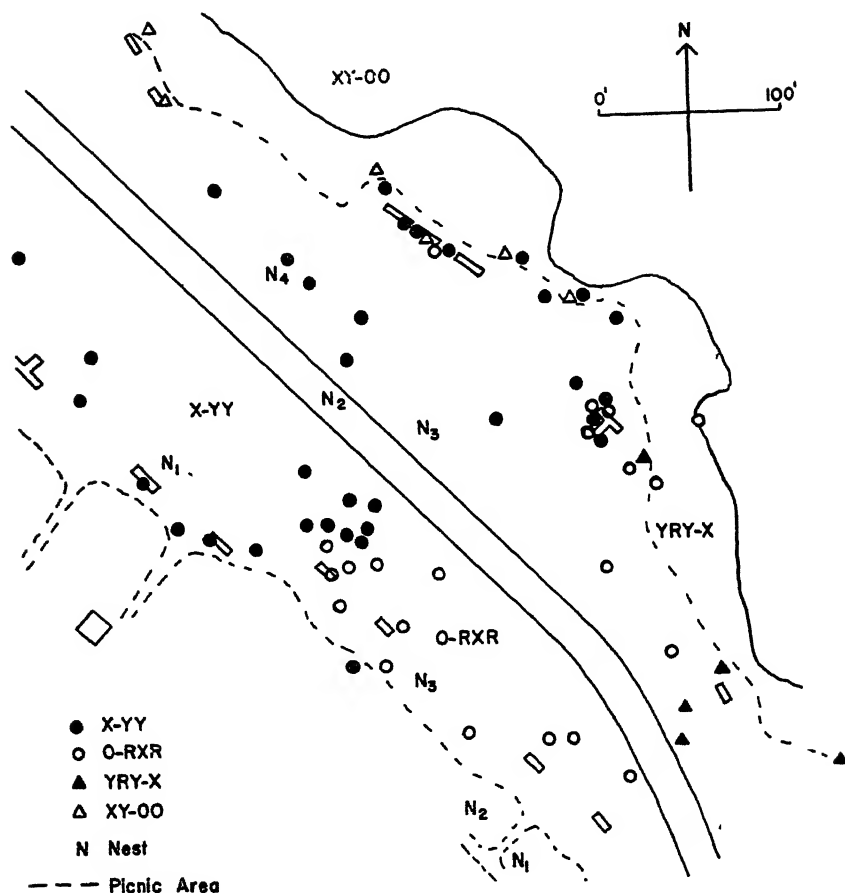


Fig. 2. Locations where Wing-spreading was performed by four territorial male Steller's jays in the spring of 1959, in Indian Camp picnic area. Overlap of plotted points is primarily the result of spatiotemporal shifts in dominance of individuals during the season.

paired and possessing territories. None of the observations were of the few birds known or suspected to be without a territory. Unpaired birds were rarely observed in Wing-spreading, with the exception of female XW-WW, who gave this display commonly in the ten-day period between losing one mate and acquiring another in December, 1959. However, unlike most unpaired jays, she had a strong territorial attachment, resulting from her long period of being paired to her earlier mate (X-YY). The slight increase in the frequency of Wing-spreading by XW-WW at this time seemed to be stimulated not by the process of finding another mate, but by an increase in the number of intrusions into her territory by other jays, which increase in turn resulted in part from the fact that sunflower seeds were put out by the investigator as bait, but especially from the absence of the formerly dominant male (X-YY).

Location.—When the locations where Wing-spreading was observed were plotted on a map, they were found to be mainly confined to the individual jay's own territory (as shown in fig. 2). Wing-spreading was not recorded more than a short distance from the territory, although both sexes frequently flew long distances into other territories.

Wing-spreading was not restricted to the nest area, the border area, or any particular area within the territory. It was usually given as a response to intruding jays, and therefore was most frequent at those places where contacts between neighboring pairs were most common. Such places were not restricted to territorial boundaries, but often occurred within a territory where food, water, or nesting material attracted jays from neighboring areas.

Agonistic situations.—The common occurrence of Wing-spreading as a territorial response indicates that with it may often be associated a degree of agonistic arousal. However, fights, chases, and supplanting attacks very rarely followed Wing-spreading. Similarly, escape behavior was uncommon following Wing-spreading. I often received the impression that the neurobehavioral mechanisms (NBM's) for attack were somehow being inhibited, or that some other type of frustration was occurring. Such impressions rely on the temporal proximity of Wing-spreading to acts which by their nature were mutually exclusive with territorial defense, such as foraging or the storing of food.

Close association with the mate may be one of these acts which inhibits the NBM's for attack. On one occasion (April 21, 1958) a male gave the display at other jays which were on a picnic table beneath his nest. Despite this male's lack of attack or other indications of strong arousal (e.g., "threats") which would normally have been expected, the other jays soon left. Then the male quickly obtained an item of food and flew to the nest, where he fed the female. In this case it would appear that the NBM's for feeding the female competed with the NBM's for defending the nest area, and hence resulted in a less vigorous response to the intruding jays near the nest.

A more common case of association with the opposite sex in the same temporal sequence with Wing-spreading occurred during territorial encounters between pairs at the mutual border of their territories. In such situations one or all of the birds gave the Wing-spreading display, and usually all of them gave some variation of the Guttural call. Other pairs or individuals were sometimes attracted also. The defending males typically perched 6–12 inches from their own females, and the two opposing males one or more feet apart from each other, with their females slightly farther apart, so that the males often were between the females. As the excitement declined, such pairs frequently showed indications of actual courtship behavior; and, in fact, full-intensity courtship displays were normally preceded by Wing-spreading and Gutturals in groups of excited birds. Such groups may be homologous to the "courtship parties" or "spring gatherings" observed in some other species of jays (e.g., *Cyanocitta cristata*, *Garrulus glandarius*) (Hardy, 1961; Goodwin, 1951). Thus, Wing-spreading was frequently associated with sexual behavior and with a low frequency of attack.

Behavioral contexts suggest that other types of frustration arising from competing NBM's may also have elicited Wing-spreading. Birds carrying twigs or

other nesting material sometimes gave the display with the material still in their bills. It was not uncommon to observe that a bird who had just filled its mouth with sunflower seeds would give the Wing-spreading display previous to storing the seeds, but that on his return, having disposed of the seeds and being presumably uninhibited by the NBM's for storing, he would supplant or chase away the jays who previously had elicited the Wing-spreading.

Avoidance of a dominant opponent also appeared to conflict with NBM's for aggression. Jays who had been supplanted just outside their area of dominance sometimes showed Wing-spreading afterward, either near the location of the encounter or after returning to their own territories. Similarly, after fighting or other types of high-arousal aggressive encounters, one or both opponents sometimes retreated toward their own territories and performed Wing-spreading. A similar conflict between NBM's for territory defense and avoidance of the opponent was probably also present in many of the encounters in which pairs met and gave the Wing-spreading display at their mutual territorial boundary.

Other situations.—All the contexts mentioned above seem to involve situations which typically elicited territorial defense or other overt aggressiveness; however, Wing-spreading was sometimes observed in contexts which suggested that activation of defense NBM's was not necessarily importantly involved. On a few occasions jays gave this display while eyeing the bait inside a trap. And certain individuals, who learned to follow me when I arrived in the morning until I put out bait, would commonly display at me, then cease and immediately fly to the bait when it was offered. They would even follow me into neighboring territories; this suggests that the display was probably not a form of defense of territory, but more likely resulted from frustration of aroused NBM's for feeding.

Temporary desynchronization of coöperative reproductive activities appeared also to elicit Wing-spreading. Aggression between members of a pair was not normally observed in the nest-building phase, so it could not have been an important factor in causing the display in these situations. Typically, mated Steller's jays accompanied each other when building their nests and throughout the intervening periods of foraging. Occasionally one jay might cease foraging and seek to renew nest building before its mate was ready. Such a bird might show mild Wing-spreading directed at its mate until the mate accompanied it on the flight for nesting material.

The display was also used by jays while visiting a potential nest site. During the first few days of pair formation between female XW-WW and male RV-VRX, in December, 1959, XW-WW was seen to go to a site where a little nesting material had accumulated and give this display. Her new mate then went to her on the nest and courtship feeding seemed to occur there. In the early part of the breeding season, RV-VRX, at the same site, spread and fluttered his wings, meanwhile uttering a high-pitched, squeaking sound unlike the *aap* that normally accompanies this display. He then manipulated nesting materials briefly. Later in the same day, XW-WW was seen Wing-spreading first at the same site and then at another likely-looking nest site, where she was fed by RV-VRX. More Wing-spreading in potential nest sites by RV-VRX was seen the same day. During all these displays there was no evidence of the presence of rival jays who might have elicited them.

Later, another male, actually building, was seen giving the display on his nest just after bringing mud to it. Males were never seen displaying on the nest when territorial defense was involved. They would first approach the intruder. Only rarely was such a low-level response given to intruders so close to the nest.

INTEGRATION WITH OTHER BEHAVIOR

From these considerations the conclusion is suggested that Wing-spreading was elicited in a rather wide variety of contexts, all involving a moderate or low level of arousal (compared to fighting or strong threat). Behavioral NBM's which have been inferred from observation as conflicting with each other and as eliciting the Wing-spreading display include, in various combinations, those for supplanting, territory defense (attack), feeding of the female, courtship, carrying of nest material, storage of food, avoidance of a rival (escape), foraging for nest material, and demonstration of nest sites. Common to all contexts is a condition of mutual exclusion between opposing behavioral types, or the blocking or prevention of a behavior pattern by environmental factors.

On the basis of such observations, the hypothesis could be proposed that the areas of central nervous localization of Wing-spreading may be activated by a rather wide variety of inputs, and that these are not restricted to the two types (attack NBM's and escape NBM's) sometimes proposed by other authors for displays given in similar contexts in other species. Perhaps the relatively low level of behavioral arousal and probably of neural activation required for Wing-spreading allows it to be elicited by a wider variety of neural inputs than does other agonistic behavior requiring a higher level of arousal. Such a hypothesis would explain the great variety of inputs capable of arousing low-level displays as compared with high-level displays and behavior.

EFFECTS ON BEHAVIOR OF OTHER JAYS

Determining the effects of the Wing-spreading display on the behavior of birds that have witnessed it was difficult. Frequently, such factors as location in respect to territorial borders, individual recognition, sex, dominance phenomena, and the behavioral context of the display had greater influence on the behavior of the observing bird than the display itself had.

Because Wing-spreading was employed in a diverse variety of behavioral contexts, it must have either a very general effect or multiple specific effects, depending on the particular context. In practice it has not been possible to separate these alternatives. A theory requiring few assumptions would be that the conspicuous position and movements of the wings in combination with the calls which invariably accompanied them, serve primarily to draw greater attention to the displaying bird. This should also have the effect of increasing the awareness of the observing bird of the entire behavioral context, thereby possibly, though not necessarily, influencing his behavior.

A few observations have already been mentioned concerning changes in behavior immediately after a jay's witnessing of the act of Wing-spreading. Various types of synchronization of nesting and sexual behavior seem to have been facilitated. Courtship feeding may have been stimulated. In aggressive encounters the

effects were variable; at some times, opponents flew away just after seeing the display, and at other times, paid little attention. Usually the reaction of the opponent was correlated with his dominance relationship to the displaying bird at that particular site. If he was subordinate, the display sometimes stimulated him to leave; if dominant, he remained.

WING-FLICKING

FORM

Wing-flicking in the Steller's jay was basically like wing-flicking in other passerines. It seemed to consist of the initial movements used in taking flight, in contrast to low-intensity Wing-spreading, which did not give this appearance. The wings were jerked very rapidly off the back for a slight distance, and as quickly returned; in low-amplitude Wing-spreading, the movements were not as fast and the wings might be held away from the body for a variable length of time.

The crest angle was typically high during Wing-flicking, the mean of 29 observations in table 4 being 63 degrees, and the mode 70 degrees. In contrast, the crest angle during Wing-spreading averaged 39 degrees in 44 observations at intensity

TABLE 4
CORRELATION OF INTENSITY OF CREST ERECTION WITH INTENSITY OF TAIL-FLICKING,
TAIL-SPREADING, AND WING-FLICKING

Type and intensity of action		Degrees of elevation of crest											
		0	10	20	30	40	50	60	70	80	90	N	Mean degrees
Tail flicking.....	0	59	34	63	78	37	19	20	16	9	..	335	28
	1	..	3	4	10	11	5	8	7	1	1	50	45
	2	1	5	4	15	25	19	9	2	80	60
	3	5	6	4	33	39	15	1	103	64
	T	59	37	68	98	58	43	86	81	34	4	568	..
Tail-spreading.....	0	55	34	59	82	50	41	71	66	22	2	482	39
	1	3	4	4	7	4	2	4	8	3	..	39	42
	2	1	1	2	4	3	..	3	2	1	1	18	43
	3	..	1	..	3	2	2	1	1	4	..	14	52
	T	59	40	65	96	59	45	79	77	30	3	553	..
Tail-spreading without tail-flicking.....	0	56	30	56	66	32	19	17	14	6	..	296	27
	1	3	3	3	7	3	..	1	1	21	26
	2, 3	..	1	2	2	1	..	2	..	3	..	11	46
Wing-flicking without Gutturals.....		..	1	..	3	2	1	6	7	6	3	29	63

NOTE: Observations of all types of behavior (e.g., vocalizations, displays, comfort acts, etc.) are pooled. Therefore, horizontal comparisons at one intensity rank are less reliable than vertical comparisons. For each observation an estimate of crest angle was made, and wherever possible the intensity of movement and extent of spreading of tail and wings were scored, on an arbitrary rating scale of four ranks: 0 = none, 1 = slight, 2 = moderate, 3 = extreme. Adjacent intensity levels, therefore, overlap to some extent. Specifically, tail-flicking was scored as follows: 0 = no movement, 1 = no rapid jerks, but a few flicks at small amplitude, 2 = one or more rapid jerks at small amplitude, 3 = three or more rapid jerks of wide amplitude. Values in the table represent actual numbers of observations, not percentages.

levels 0 and 1 combined, and averaged 37 degrees in 131 observations at intensity levels 2 and 3 combined, the modes being 20 and 40 degrees respectively.

When the wings were flicked, the tail was almost invariably flicked as well. An indication of the relationship is shown in table 5. However, tail-flicking occurred much more commonly without than with Wing-flicking.

TABLE 5
CORRELATIONS BETWEEN OCCURRENCE OF WING-FLICKING AND INTENSITIES OF
TAIL-FLICKING AND TAIL-SPREADING IN THE STELLER'S JAY

Intensity of tail action		Occurrence of Wing-flicking—all observations		
		0	1-3	N
Tail-flicking.....	0	268	..	268
	1	30	1	31
	2	59	9	68
	3	66	6	72
	N	423	16	439
Tail-spreading.....	0	384	15	399
	1	30	7	37
	2	11	..	11
	3	6	.	6
	N	431	22	453

NOTE: The intensity scale is explained under table 4.

Of the 54 occurrences of tail-spreading recorded in table 5, 7 were accompanied by Wing-flicking; but proportion of occurrences of Wing-flicking which were accompanied by tail-spreading is higher, the number amounting to about one-third of the 22 records.

CONTEXTS

When Wing-flicking was observed, it was generally in the extreme manifestation of the contexts in which tail-flicking occurred. It was most consistently seen in jays that had just alighted in a tree after release from banding. Of the 33 observations of jays just released in which Wing-flicking was looked for, it was present in 25 and absent in 8. Tail-flicking was present on all of the 29 occasions on which I watched for its presence or absence in conjunction with Wing-flicking. As is indicated in table 22, jays that called in the same circumstances (just after alighting from release) usually gave *Wah*'s (in 17 of 21 observations). Jays that had just landed on picnic tables or other places associated with strong agonistic arousal, also Wing-flicked at times, but less consistently than after release from banding.

Wing-flicking was commonly observed in those jays which were exceptionally active in mobbing. And in this context also, *Wah*'s were the predominant call.

On a few occasions jays were seen to flick their wings just after hearing a door slam or hearing other loud and sudden noises. The resemblance of Wing-flicking to the initial elements of the motor pattern of taking flight was especially strong on these occasions.

INTEGRATION WITH OTHER BEHAVIOR

Because of the occurrence of Wing-flicking in the extreme manifestations of the contexts in which tail-flicking was evoked, and generally only at the higher intensities of tail-flicking, a simple hypothesis concerning their integration with each other would be that the neural pathways of these two acts share a common central population of neurons. Activation of this common population at low intensities would, according to this hypothesis, yield tail-flicking; at higher intensities it would yield tail-flicking plus Wing-flicking; and at still higher intensities it would yield the fully formed elements of taking flight. The observations are in agreement with this hypothesis, but the neural mechanisms remain to be explored.

In degree of crest erection, tail-flicking and Wing-flicking also showed evidence of coördination. The average and modal crest angles for Wing-flicking, 63 and 70 degrees respectively, are very close to the comparable values for tail-flicking at intensity level 3, which are 64 and 70 degrees respectively (table 4). The relationship is additional evidence for the commonality of the neural events which control Wing-flicking and high-intensity tail-flicking. The *Wah*, which was the most frequent call given during Wing-flicking, also was similar in crest-angle distribution, although it was given in a wide variety of other contexts too; the mean and modal values are 59 and 70 degrees respectively (fig. 8).

The limitations of Wing-flicking as an indicator of activation of escape NBM's are similar to those discussed in connection with tail-flicking.

GAPING AND APPEASEMENT BEGGING

Gaping and appeasement begging were only rarely observed; they were recorded on only about 14 days in the course of the entire study. They were most common in the months from February through October when the proportion of the population without territorial attachment was relatively high and groups of nonbreeding or postbreeding jays accumulated around local food sources.

In behavioral form and accompanying vocalization, appeasement begging resembled the begging of juveniles for food, but it was rarely observed at high intensities of wing-fluttering, and it was characterized by withdrawal from the jay to which it was given, rather than by approach toward him.

So far as appeasement begging involved flicking or fluttering of the wings, it may be said to have resembled Wing-spreading, but it differed in the following ways: (1) It was employed usually in competition over a food source. (2) It was performed at much closer range (a few inches to a few feet, rather than 5-20 feet). (3) It was generally performed not by mated birds on their territories, but by unmated birds within the territory of another jay. (4) It was often preceded by a retreat of a few steps. (5) A crouched position was employed, in which the body was close to horizontal and the tail was pressed against the substrate, if such begging took place on a flat surface. However, a gaping bird on a table edge was sometimes forced by the advance of his opponent to lean backwards to a vertical position, and eventually to lose his balance and fly. (6) The head and neck were retracted onto the shoulders. (7) Gaping with the bill open as much as 1.5 cm was characteristic, and the opened bill was sometimes used to parry attacking bill

thrusts by the opponent. (8) The associated call note was *Wah*, as in juvenile begging, rather than *Ow* or a Guttural call, as it was in Wing-spreading.

Appeasement begging, or gaping, was recorded in two known males and two known females. All individuals observed in such behavior, both unbanded and color-banded, were far below the top of the dominance hierarchy. It was perhaps their subordinate position and probable lack of a territory of their own which led them to tolerate such close proximity to dominant jays in an attempt to obtain food, even though this led to attacks from these jays.

Jays were observed gaping while approaching others at bait and supplanting them, but more often appeasement behavior was observed after a jay, in his attempt to obtain food, had approached another jay too closely and had provoked an attack. In such instances, the short retreat followed by crouching, gaping, wing-fluttering, and the giving of the *Wah* call, was often apparently successful in inhibiting the dominant's attack; and if not, the subsequent bill thrusts could be parried by the appeasing bird's gape. The effect of such appeasement behavior thus appeared to be to allow subordinate jays to approach food sources closely and more often by inhibiting the inevitable attack which such close approaches generally elicited from dominant jays.

Although appeasement behavior as observed in the study area was in the context of competition for food, it should not be presumed that it would not also occur in other contexts. An unmated male (OGO-OX) who persisted in remaining in the territory of male X-YY was several times seen fluttering his wings silently, with his bill closed and vibrating his tail rapidly up and down through a 15-degree arc, while X-YY called aggressively and bill-rapped a few feet away. The unmated jay was subsequently chased from the territory by X-YY, but the display seemed to inhibit X-YY's attack temporarily. Jays confined in aviaries seemed more prone to appeasement behavior because of their frequent proximity to dominants in a variety of contexts.

The display of mated females when soliciting courtship feeding was similar to appeasement begging, in that such females crouched with open gape and sometimes with fluttering wings, but the *Wah* was never given by them and the male was attempting to give food to the female rather than to attack her.

AGGRESSIVE SIDLING

Aggressive Sidling was a posture that was important in almost all closely contested aggressive encounters between individual jays. It was one of the two displays of the Steller's jay that resembled the "lateral display" of *Garrulus glandarius*, as described by Goodwin (1949, 1951, 1952, 1956) and as discussed below.

COMPARISON WITH SEXUAL SIDLING

The two stereotyped postures which resembled the lateral display of *Garrulus* will be referred to as Aggressive Sidling and Sexual Sidling. Aggressive Sidling is illustrated in figure 9. The two forms of sidling resembled each other in the following ways: (1) The displaying bird was typically oriented laterally to the opponent. Thus, when two jays gave this display at each other they were parallel; however, they might face either in the same or in opposite directions. (2) Reversal

of direction commonly occurred in such a way that a jay facing in the same direction as its partner or opponent would make a 180-degree jump to face in the opposite direction. (3) The tail could sometimes be spread moderately, and (4) could be turned at the base toward the other bird. This turning was most conspicuous just after a jay reversed his direction, when his tail was shifted from one side to the other. (5) The upper side of the tail and body could be turned slightly

TABLE 6

DIFFERENCES BETWEEN AGGRESSIVE SIDLING AND SEXUAL SIDLING IN THE STELLER'S JAY

Characteristic	Aggressive Sidling	Sexual Sidling
Crest (figs. 3 and 6).....	Generally 50-90 degrees	Generally, 0-20 degrees
Body posture (fig. 9).....	Head frequently extended or rapidly lowered (bowing) Body often more horizontal Legs often flexed in crouch	Head maintained upright Body in normal attitude Legs not flexed in crouch
Actions.....	Vigorous, intense	Restrained, subdued
Vocalizations (table 21).....	<i>Shook</i> common in both sexes Musical occurs in males Rattle occurs in females	Song usual Musical uncommon Rattle also occurs
Displacement behavior.....	Abundant bill-rapping and displacement digging	Absent or rare
Sex of jay eliciting display....	Generally same	Opposite in all of many observations
Associated behavior.....	Fighting	Elements of courtship: Circling, probing, mounting
Behavior of opponent or partner.....	Generally Aggressive Sidling	Generally motionless; occasionally Rattle or Song

toward the opponent or partner. (6) The head and bill were turned slightly toward the partner or opponent. (7) The distance between the displaying jays was typically 6-12 inches.

The differences between Aggressive Sidling and Sexual Sidling are indicated in table 6. No difficulty was ever encountered in distinguishing between them, and they did not normally intergrade.

COMPARISON WITH LATERAL DISPLAY OF *GARRULUS*

Both Aggressive Sidling and Sexual Sidling differed from the lateral display of *Garrulus*, as the latter is described by Goodwin (in all four of the works cited just above), in these ways: (1) The feathers of the rump, flanks, and belly were not noticeably more erect than the plumage of other body areas, nor were the feathers of the back and upper breast noticeably depressed. There was no conspicuous feather erection on the body. (2) The wings were not drooped noticeably, nor did the secondaries seem any more exposed than in normal perching positions. Therefore, because fewer elements were involved in the comparable displays of

the Steller's jay, the display of *Garrulus* may be considered to be more specialized, evolutionarily, than that of the Steller's jay, as is its wing pattern.

The two forms of sidling in the Steller's jay were similar to the lateral display of *Garrulus* in the following ways: (1) The displaying jay tended to be oriented laterally toward the animal eliciting the display. (2) The head could be extended forward. (3) During aggressive contexts, high-intensity calls were given, such as the *Shook* in the Steller's jay and mimicry or "hissing sounds" in *Garrulus*; or, in females, the Rattle in the Steller's jay and the "castanet-note" or "clicking-sounds" in *Garrulus*. (4) Low-intensity vocalizations, such as the Song (see below) in the Steller's jay and "soft notes in a variety of (usually) squeaky, bubbling sounds" (Goodwin, 1956:193) in *Garrulus*, were given in courtship contexts. (5) Displacement activities were interspersed in aggressive contexts. (6) Both aggressive and sexual forms of the sidling and lateral displays were prominent in both species during the "spring gatherings." (7) Crest erection was prominent in contexts involving "increased conflict" and was shown "when both or all of the opposing drives" were "stronger" (Goodwin, 1956:192). Therefore, crest erection in *Garrulus* occurred during high-intensity agonistic contexts as it did in the Aggressive Sidling of the Steller's jay. My few observations of *Garrulus* courtship in London suggest that the crest is typically depressed in *Garrulus* when in courtship, as it was in the Steller's jay in Sexual Sidling.

ADDITIONAL DESCRIPTION OF THE FORM OF THE DISPLAY

The crest in Aggressive Sidling was typically 60 degrees high or higher (86 per cent of 78 observations in fig. 6). The few observations of low crest angles which I recorded were mostly associated with the raising of the plumage of the back—a rarely observed behavior confined primarily to one female jay and discussed in more detail below (see subsection entitled Raising of the Back).

The extension of the head during Aggressive Sidling seemed to be correlated with the loud calling that accompanied the posture, since it did not necessarily occur at other times. The head was also sometimes suddenly lowered and the tail was flicked upward (bowing). Bowing was similar to incomplete displacement digging or bill-rapping, but it also resembled the motions of Steller's jays when mobbing an owl. Daanje (1951:87), in a discussion of the derivation of displays from incomplete locomotor movements, drew attention to a bow of *Garrulus* that is used in temporal proximity to fights (as is Aggressive Sidling).

VOCALIZATIONS, SEX, AND STATUS OF PARTICIPANTS

I made no attempt to keep a record of the exact proportion of individuals of each sex observed in Aggressive Sidling, but the data gathered during observations of crest angles in Aggressive Sidling show that the individuals participating were male in 65 of 73 recorded instances in which the sex was known. Another set of data on the calls given during Aggressive Sidling (which has many records in common with the data above) shows that in 90 to 95 observations when the sex was known the caller was a male. That is to say, Aggressive Sidling was observed roughly 9 or 10 times as often in males as it was in females. No differences between sexes in the form of the display were noted, although such differences in *Garrulus*

have been reported (Goodwin, 1949:279; 1951:416). The jays engaged in Aggressive Sidling were virtually all paired, territorial birds. I did not see jays which I thought were unpaired or juvenile performing this activity.

The vocalizations given during the process of Aggressive Sidling are recorded in table 21. In the male, *Shook* was the call most frequently used, although a wide variety of others were used.

It was observed that when both opponents were calling they usually gave the same call, regardless of what that particular call happened to be. And when one jay switched to a different call, the other jay would, too. The probability of giving the same calls was highest when neither opponent retreated or advanced. But, when the display occurred after a chase, or when one jay was definitely advancing, the calls of the two participants were more often different.

CONTEXTS

Aggressive Sidling was the most common behavior immediately following a fight (but not a supplanting attack) and also, sometimes, preceded fighting. Because of the wide overlap of the foraging areas of the many members of the jay population, especially in the nonbreeding season, individuals often encountered others whose actual or potential rank in the dominance hierarchy at a particular locus was similar to their own. When two such individuals met, the question of dominance was often determined during Aggressive Sidling, the dominant jay advancing and the subordinate one gradually retreating.

Jays sometimes gained access to bait set out on picnic tables by this method of slow, threatening approach, rather than by the more common method of supplanting. Aggressive Sidling was also observed to be common in jays contesting natural food sources or foraging spots. In this context the display was seen at all seasons.

Although at all seasons I observed avoidance behavior which indicated that jays were aware of individual dominance relationships with many other jays in relation to the location of the encounters (i.e., in relation to territories), the awareness became more intense in March and April as the breeding season approached: jays were more cautious in flying through territories other than their own, and were quicker in leaving when threatened. Also, the attacks and threats made at intruders by settled jays within their own territories were more intense and frequent. Correlated with this period of increased intensity of agonistic behavior, Aggressive Sidling too became more frequent.

When not stimulated by a dispute over food, Aggressive Sidling was usually localized spatially in the zones where the areas of dominance of neighboring males apposed. Therefore, it occurred at places and times in which neither jay was completely dominant. In locations not belonging to one male there was little advancing or retreating of the opponents; but when the mutual displaying began well inside a territory, the dominant jay would advance and the subordinate one would retreat sideways toward his own domain.

When the females were incubating, Aggressive Sidling sometimes occurred between two males at their mutual territorial borders, and these instances furnish evidence that the aggressiveness shown by the participants was in defense of

areas in which they were dominant, rather than in defense of specific food items, nests, or females. Females commonly accompanied their males in border disputes, at times other than incubation and brooding periods, and when the females were present it was not possible for me to determine whether the dispute was in defense of females or of a topographic area; the latter, however, seems more likely, to judge from the behavior of the jays and the location of disputes at a boundary zone. I did not observe Aggressive Sidling in a contest for a female; however, it should be expected to occur sometimes in the course of pair formation, when many unmated males were present. Such conditions were not observed at Indian Camp.

BEHAVIOR ELICITED BY AGGRESSIVE SIDLING

Since Aggressive Sidling usually occurred at times and places in which neither opponent was completely dominant, the usual response at boundaries was for both jays to give the display directed at each other for as long as eight to ten minutes or more intermittently. However, sideways retreat from the displaying jay was also frequently observed, thus illustrating the effectiveness of the total behavior pattern as a threat.

DISPLACEMENT BEHAVIOR

Displacement behavior, especially bill-rapping and digging, were conspicuous elements in the agonistic behavior of Steller's jays and may possibly have had some functional importance in that context. The forms of displacement behavior described here seem to be characteristic of the Corvidae and of other groups with similar foraging adaptations, such as the Paridae (Hinde, 1952:73).

The activities discussed below have been classed under the well-known term displacement behavior for the following reasons: (1) Being foraging movements, they were irrelevant in Aggressive Sidling and in other agonistic contexts and were, therefore, displaced from their normal context of searching for and manipulating food; (2) they were typically incomplete, in the sense of being non-functional: nuts were not opened during bill-rapping, nor was food discovered or eaten during digging; (3) their vigor, intensity, and rate of performance conspicuously exceeded the norms for functional foraging; (4) the context in all cases was one in which "conflict" between mutually exclusive consummatory acts, apparently usually attack and escape, might be inferred.

FORM

Bill-rapping.—Bill-rapping was the most conspicuous displacement behavior in the Steller's jay, although perhaps no more common than digging. In bill-rapping the jay hammered vigorously against the perch, usually between his feet if he were on a branch, or in front of him if he were on a flat surface such as a table or the ground. The movements were similar to the ones used in opening a hard object, such as an acorn, with the bill, or in peeling bark off a branch. In many close-range observations of jays that were opening acorns, laurel nuts, and sunflower seeds, only the lower mandible was used to make the initial puncturing blows, which were delivered with the bill slightly open to allow the lower mandible to strike the object while the upper one passed over the outside surface. In the

relatively few cases of displacement bill-rapping which were closely watched, the lower mandible was similarly separated from the upper one and delivered the blow. A similar opening of the bill in like circumstances occurs in scrub jay and was implied by Goodwin (1949:282) for *Garrulus*. The resemblance between displacement bill-rapping and the normal or autochthonous opening of acorns was close, except for the presence of the object.

Hinde (1952) discussed the resemblance between bill-rapping and normal foraging in tits, but hesitated to conclude that the former had been derived from the latter because the motor pattern of bill-rapping also resembles that of pecking an opponent. The same objection could be raised concerning the activities of the Steller's jay. However, it was observed a few times in the great tit (*Parus major*) (Hinde, 1952) and commonly in the Steller's jay that when the substrate changed from a perch to the ground, the displacement action became digging or leaf-turning, neither of which can be regarded as elements of the attack pattern. Therefore, the evolutionary derivation of bill-rapping from attack elements seems unlikely. It is more likely to be an evolutionary derivation from the generalized pecking used in foraging under bark, and perhaps also in opening nuts and other hard objects.

Digging.—In displacement digging, the jay quickly inserted its bill into the leaf litter, soil, or other loose substrate, and with a vigorous flip of the bill to one side tossed aside some material. The action was similar to normal foraging, except that it was typically more vigorous, more frequently and more rapidly repeated, and was not followed by close examination of the area uncovered. It is probably analogous to the displacement turning of leaves in the great tit (Hinde, 1952). I know of no observations of displacement digging or leaf-turning in other jays, except in the Mexican jay (*Aphelocoma ultramarina*) (Hardy, 1961:116), but they are to be expected. Fairly extensive observations on scrub jays have not yet revealed such behavior, possibly because of the rarity of observations of strong threat contexts on the ground in that species.

Other displacement activities.—Bill-rapping and digging were the most commonly observed displacement activities, but a variety of others were seen which are also related to foraging. Although unimportant in terms of frequency of observations, these variations indicate the plasticity of the displaced foraging behavior.

In one observation of Aggressive Sidling, two males were pecking at branches and under bark; and at another time, a jay engaged in Aggressive Sidling was seen knocking the bark off a dead twig. Prying and knocking off pieces of bark were normal foraging actions of the Steller's jay, especially in the winter, when food was scarce and when acorns were no longer commonly utilized. These observations were made in late December of 1958 and 1959, a fact that possibly indicates facilitation of this type of displaced behavior in this season. In early April I made a third observation, less easily interpreted as displacement behavior, of very active and vigorous probing and rapping with the bill under bark and in crevices of trunks and branches; but this did not occur during Aggressive Sidling, and although it seemed to be displacement behavior because of its vigor and the context, it seemed also to be merging with normal foraging.

On March 25, 1959, RV-VRX or X-YY was seen doing much bill-rapping in Aggressive Sidling, and pulling, in a vigorous, jerky fashion, on old eucalyptus berries and leaves. Four days later, male RV-VRX, in Aggressive Sidling, was seen tugging at dead leaves in the crotch of a branch. The latter type of foraging was sometimes observed in nonconflict contexts, but the former observation of pulling on eucalyptus berries and leaves was not representative of a commonly observed foraging pattern.

In April, during Aggressive Sidling two males were observed bill-rapping intently and knocking off leaves of the coast live oak by pecking at their petioles. In July, at the Hastings Reservation in Carmel Valley, a jay which had become excited by my presence grasped many small, fresh, green leaves of the Pacific madrone (*Arbutus menziesii*) individually with its bill, usually by the distal end of the petiole or the basal part of the leaf, and tried hard to pull them loose, but it succeeded only once or twice. This was done in a most vigorous and hurried manner, and ceased when (as judged on the basis of other criteria) the jay calmed down. Earlier in July I had seen a juvenile that was obviously excited by my presence grasping many leaves of the coast live oak by the middle but not pulling at them. It did not appear to be obtaining any food. These were not patterns of behavior observed in normal foraging, although they may be related to the act of removing insect larvae from leaves. "Pulling at leaves" has also been observed in the great tit (Hinde, 1953:208).

Bill-rapping has been reported "to commonly accompany nervous tension of any kind" in *Garrulus* (Goodwin, 1951:418), and could be classed as a displacement activity. In the Steller's jay, however, it was not common as a displacement activity. Once, just after an encounter involving Aggressive Sidling in which RV-VRX had been tugging at dead leaves as a displacement action, he and his mate were seen bill-wiping, although they had not been foraging or eating the leaves. This may have been a displacement reaction, but the almost imperceptible nature of the stimuli that normally elicit bill-wiping require that the possibility of normal activation of bill-wiping in this instance be left open, since the male, at least, had had his bill in contact with accumulated dead leaves and crotches of branches. Displacement bill-wiping also occurs in the blue jay (Hardy, 1961).

Song has been interpreted as a displacement act in the gray jay (*Perisoreus canadensis*) (Lawrence, 1957), but it is not considered to be a displacement act in the Steller's jay, for reasons discussed below under the heading Song.

CONTEXTS

Relation to aggression.—Displacement behavior was conspicuously associated with Aggressive Sidling, long bouts of which almost invariably included some displacement activities. However, less intense displacement activities, usually bill-rapping, were commonly seen at other times, such as when the presence of the observer was responsible for a jay's reluctance to approach a food source or a foraging area, or when the observer was raiding a nest. On March 31, 1959, male O-RXR was seen bill-rapping while his own female was incubating and a neighboring female RR-X was courting him by Sexual Sidling, Circling, and

Song. This seemed to indicate an aggressive response to RR-X, since there were no indications of sexual behavior in O-RXR.

Dependence on substrate.—The variation in displacement behavior according to the location of the jay and the material available to it has already been suggested above. Jays which were bill-rapping on a perch in a tree were commonly seen to continue pecking at the ground just after having flown to the ground, but they soon switched to digging, although the character of the aggressive encounter had changed only in its location and in the substrate upon which the jays perched.

Relation to normal foraging.—The characteristics of displacement behavior were most easily recognized during Aggressive Sidling; however, they were increasingly difficult to recognize in the behavior subsequent to Aggressive Sidling. Encounters between two males involving Aggressive Sidling at a territorial boundary zone often terminated during displacement digging. Indeed, when not disrupted by an alarm, this was the usual manner in which intense disputes ended. The jays gradually separated, continuing their vigorous digging and calling; and as they moved farther and farther apart, foraging became less intense, less frequent, and more functional, the calls became less frequent, and the crest declined in angle; in short, there was a gradual transition from Aggressive Sidling and displacement foraging to normal foraging behavior as the opponents gradually separated, working their ways into their own territories. Thus the distinction between displacement foraging and normal foraging is one of degree, since all shades of intermediacy occur. Similar observations and conclusions have been reported for the pectoral sandpiper (*Erolia melanotos*) (Hamilton, 1959:168).

ADAPTIVE SIGNIFICANCE

If displacement foraging behavior in the Steller's jay can be considered a direct rather than a coincidental result of natural selective forces, and if there are positive selective pressures for the evolutionary maintenance of displacement foraging during the context of Aggressive Sidling, then the role of displacement behavior in the gradual transition from high-level agonistic arousal to normal foraging may be significant. It was the normal pathway between these two states. For the case in which boundaries are well established and not subject to significant change by prolonged threatening bouts, such as occur in Aggressive Sidling, it would be to the advantage of the individual participants to use their time in other ways, since nothing positive would be gained by long periods spent in Aggressive Sidling at the same location. Such an effect could be positively adaptive if it also predisposed or permitted the opponent to behave similarly; and both opponents normally do show displacement foraging in an even encounter.

Thus the selective advantage in this case would not be one of relieving surplus "tensions" but of channeling the behavior into more useful modes, specifically from the stalemate of an encounter at a relatively fixed boundary into foraging. The latter, if not useful in itself, at least frees the jay for other behavior which may be more useful.

INTEGRATION OF DISPLACEMENT BEHAVIOR

The crest in displacement foraging behavior, unlike the crest in normal foraging behavior, was generally quite erect, as a comparison of figures 5 and 6 illustrates, the modal crest angles being 0 degrees for normal foraging and 80 degrees for displacement foraging (bill-rapping and digging combined). The high crest angles and the vigorous, rapid activity in displacement foraging and its occurrence during Aggressive Sidling, indicate the presence of agonistic arousal at a high level. This is probably equivalent to what various other authors have termed a high-intensity conflict of behavioral tendencies in other species.

The field observations indicate that foraging behavior was activated at high levels of agonistic arousal. But whether this relationship is caused by spatial proximity of localization of function in the central nervous system or by more circuitous neural connections has not been determined. However, the information on localization of function in the brain stem of the cat reveals a close spatial proximity of equally unrelated functions (e.g., flight, defense, and elements of finding and eating food are localized in the same area; Hess, 1957:69).

RAISING OF THE BACK

POSTURE

Raising of the back typically consisted of erection of the feathers of the dorsal tract on the back, resulting in a hunchbacked appearance. This effect was produced purely by feather erection, and did not involve any movement of other parts of the body, although the head might be lowered slightly and the bill turned down. The rump feathers were never seen to be erected, but the feathers dorsal to the neck were sometimes ruffled. Usually the jay was oriented sideways to its opponent, as in Aggressive Sidling. The tail was generally not flicked, although it was commonly spread, and the wings were not observed to be flicked at all. The body tended to be more horizontal than normally. The distribution of observed crest angles is shown in figure 6 and discussed in the subsection Crest Movements, below.

CONTEXTS

This display was only rarely observed. Virtually all observations of jays erecting their back plumage were made during the nonbreeding season, at a picnic table on which sunflower seeds had been placed for bait. All were in aggressive contexts. In 33 observed encounters in which the plumage of the back was erected, 26 of the jays were supplanting others, 5 jays were in indecisive encounters, and 2 were subsequently supplanted by the jay that had elicited the display. Of these 33 observations, 27 were of females and 6 of males. On 12 occasions it was recorded that no call was given; on 20 occasions no record was made of whether a call was given or not; and on only 1 occasion was any vocalization recorded: this call was the Musical. The display was usually given silently.

TAIL MOVEMENTS

VERTICAL MOVEMENTS

Form.—In tail-flicking the tail was jerked rapidly upward and then slowly lowered. When tail-spreading occurred concurrently, the tail was spread and then folded before the end of the quick upward phase. The head and body were sometimes rapidly lowered while the tail was in the upward phase of its movement. Call notes and jerky movements such as Wing-flicking also occurred mainly in the course of the upward phase. The tail could be flicked as many as forty-five flicks per minute, although rarely for as long as one minute at that rate. After the jay alighted, its tail was often flicked even more rapidly for a few seconds; then the rate of flicking quickly declined.

When a jay was jumping along the ground while foraging, its tail could be raised to a few degrees above horizontal with each jump, and gradually lowered to below horizontal between jumps. A photograph of a jay taking flight shows the tail raised to 45 degrees above the horizontal line which passes through the long axis of the body. The legs are fully extended, the wings raised, and the feet just leaving the table less than an inch below. This suggests that in hasty and vigorous take-offs such as this one in which the bird was being supplanted by a scrub jay, a rapid and extensive upswing of the tail and wings occurred simultaneously with the initial push-off from the legs, thus allowing a downward movement of the spread tail and wings immediately after the initial leap from the table.

When the jay was engaged in opening acorns or sunflower seeds, its tail was often raised to a position near horizontal during the vigorous action of breaking open the outer shell, but was allowed to drop gradually downward when the bird's head was held high or when the jay was pulling off chunks to swallow—a less vigorous activity requiring less muscular tension.

Generally, the strong upward flick of the tail seemed coincident with one or more of a number of sudden and vigorous movements, such as calling, Wing-flicking, jumping, and taking flight. A relatively high position of the tail, near horizontal, seemed to be associated with a general tenseness of muscles, as in alighting or the opening of acorns; and a low position, near vertical, with relaxation, as in sleep or preening.

The tail was also moved in a vertical plane in a variety of other contexts. The usual method of attacking another jay was to fly at it and attempt to flutter above it while pecking at it. Jays making frontal approaches to an opponent, but not direct attacks, often had their tails spread and pressed against the ground while they were standing upright in a position to peck downwards. The tail was used as a brace by being pressed against the ground while the bird was bathing in water or sun bathing. Just before defecation, the tail was usually raised 10 to 30 degrees, and afterward it returned gradually downward. While the Song was being delivered, the jay's tail was occasionally moved slowly back and forth through an arc of about a centimeter or less. When the cloacal protuberance of a jay held in the hand was pressed lightly, the bird would typically depress its tail ventrally and partly spread the tail; the legs might also be extended at the

TABLE 7
CORRELATIONS BETWEEN INTENSITIES OF TAIL-FLICKING AND TAIL-SPREADING IN
DIFFERENT CALLS AND OTHER BEHAVIOR OF THE STELLER'S JAY

Intensity of tail-flicking with particular vocalization		Intensity of tail-spreading				
		0	1	2	3	T
Total, all observations.....	0	303	20	7	4	334
	1	40	6	2	..	48
	2	64	6	2	1	73
	3	70	11	..	1	82
	T	477	43	11	6	537
Wah.....	0	8	8
	1	4	4
	2	23	3	1	1	28
	3	31	7	..	1	39
	T	66	10	1	2	79
Rattle.....	0	26	11	5	2	44
	1	1	1	2
	2
	3
	T	27	12	5	2	46
Guttural.....	0	64	3	67
	1	11	1	12
	2	8	1	9
	3	7	1	8
	T	90	6	96
Shook.....	0	17	1	..	2	20
	1	2	..	2	..	4
	2	1	1	1	..	3
	3	3	1	4
	T	23	3	3	2	31

NOTE: The intensity scales are explained under table 4. Tail-spreading given at the zero intensity level of tail-flicking is of the static or depressed type; tail-spreading given at intensities 1 to 3 of tail-flicking is of the upward type (see text).

same time. A ventral depression of the tail could also be obtained by blowing on the belly of the jays held on their backs in the observer's hand.

Contexts of tail-flicking.—Some of the contexts of tail-flicking have been indicated above. The most common one occurred just after the bird had alighted, in a situation which (as judged by other behavior) was characterized by great alertness. The tail was almost invariably flicked during a mobbing encounter. The high frequency of tail-flicking while *Wah*'s were being delivered (tables 7 and 14) makes it reasonable to consider the description of the contexts in which

Wah's occur, as applicable also to tail-flicking. However, the range of contexts in which tail-flicking occurred was much wider than the range in which the *Wah* occurred.

Integration of tail-flicking.—The integration of tail-flicking is related to the level of agonistic arousal and to attack and escape behavior. It is also apparently related to the preparation for flight, although repeated tail-flicking did not generally precede taking flight in nonagonistic situations.

Agonistic arousal.—If the intensity of tail-flicking is correlated with the level of agonistic arousal, the intensity of tail-flicking should increase with higher angles of elevation of the crest (see the discussions of agonistic arousal and of crest elevation in the next main subsection below, *Crest Movements*). That it did generally increase with a steepening of the crest angle is shown in table 4. At succeeding higher levels of crest elevation, the proportion of observations in which tail-flicking occurred increases, from 0 per cent at 0 degrees to 100 per cent at 90 degrees. Furthermore, the proportion of records at higher intensities of tail-flicking is greater at the higher crest angles (60–80 degrees) than at lower angles (20–40 degrees). The means also show an increase in crest angle with intensity of tail-flicking.

Although a correlation exists between the intensity of tail-flicking and elevation of the crest, the extent of variation between observations at similar crest angles and at similar intensities of tail-flicking implies that certain integrating factors in addition to the mechanisms of agonistic arousal are operating. The association of tail-flicking with general somatic muscular tension, and of crest elevation with autonomic innervation and smooth muscle tension, may be one reason for the lack of complete correlation between tail and crest position, since the somatic and autonomic systems are frequently out of phase because of the lag, or "tracking error," inherent with the greater employment of tonic control mechanisms in the autonomic system.

Attack and escape NBM's.—Tail-flicking in passerines has been interpreted as being indicative of a tendency to fly that is thwarted by an incompatible tendency (Andrew, 1956:179). Because of the normal association of tail-flicking with alighting and with contexts in which take-offs may be required at any moment (e.g., mobbing), tail-flicking in the Steller's jay may be interpreted as the result of low-level activation of the neural pathways controlling vertical movements of the tail which find their primary function during jumps, take-offs, and landings. Such an interpretation agrees essentially with the interpretations of Daanje (1951) and Andrew (*ibid.*).

Since flight was a conspicuous element in the attacking and fighting of jays, as well as in escaping, tail-flicking alone cannot, in particular situations observed, safely be interpreted as indicating dominance of the NBM's for either activity. Furthermore, tail flicks were not common accompaniments to *Musicals* and *Rattles* (table 14), which, rather, were usually associated with actual attacks or with a hesitation to attack; however, these calls and supplanting attacks were typified by a low level of agonistic arousal as indicated by the associated crest angles (figs. 7 and 8). Thus, the infrequency of tail-flicking during the utterance of

Musicals and Rattles might be due merely to the low arousal level, rather than to low activity of escape NBM's in particular.

In jays landing alone on picnic tables outside their territories, and sometimes within those areas, high crest angles and intense tail-flicking were often observed; and in this case NBM's for escape seemed to be competing with NBM's for remaining at the bait, but not with NBM's for attack, since there was nothing to attack. In such situations, tail-flicking, crest elevations, and the theoretical agonistic arousal which accompanied them, appeared to be associated with activation of the escape NBM's, whereas the attack NBM's were less active. Consideration of these observations alone would lead to the interpretation that tail-flicking and crest erection are correlated with activation of escape NBM's. However, the normal occurrence of crest erection and the use of the tail in fighting and in Aggressive Sidling show that tail-flicking and crest erection did not necessarily indicate a dominance of escape NBM's.

HORIZONTAL MOVEMENTS

Spreading, turning, and tilting of the tail.—Spreading, turning, and tilting of the tail were conspicuous when they occurred, because of the larger surface area or the asymmetry which they created. Generally, they were not employed alone but were used in conjunction with other signal movements in threat or courtship.

Position and contexts.—The tail was spread in postures approaching a horizontal crouch, or with the body nearly vertical, in flight (gliding), and in a variety of other postures.

In one group of activities there was a downward force exerted on the tail during tail-spreading. This was commonly observed during alighting. In birds that were sun-bathing, the tail was frequently fully spread and braced or laid against the ground. Similarly, while a jay was bathing in water the tail was also often fully spread and was braced against the bottom of the shallow pool. The spread tail was also seen in use as a brace when a jay was clinging to a vertical tree trunk and was foraging with its bill in the crotch of a branch. When the cloacal protuberance of a jay in the hand was touched, the tail was bent ventrally and spread. The tail was sometimes spread by a jay in the activities of supplanting or threatening, especially during and just after alighting; and in these cases the tail was often depressed strongly against the table, never raised. When one jay supplanting another approached the subordinate slowly by small jumps rather than by direct flight or running, the dominant bird often stood very tall and pressed its spread tail downward, at the same time aiming its bill down toward the opponent, and sometimes calling. In a jay seen just before it flew up fighting with another jay, the tail was spread and was pressed against the ground. The frequency of tail-spreading was much higher in Rattles than in any other vocalization (table 14), and in these cases the tail was either tensed or depressed, but generally not raised or flicked.

In a second group of activities, the tail was characteristically flicked upward while being spread. These activities include tail-spreading during the utterance

of the *Wah*, and in the act of mobbing, and sometimes with *Shook*'s. In mobbing, I sometimes saw the jay nearest to the owl spread its tail progressively as it approached more closely. Usually, however, the tail was both spread and folded before completion of the upward phase of a tail-flick.

A third group of behavior patterns in which tail-spreading occurred was characterized by the turning of the tail of the displaying jay toward the jay eliciting the display. In courtship, when one jay, usually a male, was Circling or Sidling to another, usually a female, the bill and tail were usually turned inward toward the female and the tail was somewhat spread. In the most fully developed form of tail-spreading in this context the wings and tail were almost fully spread and were tilted toward the female in such a way as to afford her a view of the dorsal surface while the male Circled around her. In Aggressive Sidling, jays also spread their tails slightly sometimes, at the same time turning and tilting them slightly toward their opponents.

Integration with other behavior.—Since both tail-flicking and tail-spreading were related to the acts of taking flight and alighting, they might be expected to show a close association with each other. Table 7, however, shows that 31 of 60 observations of tail-spreading occurred unaccompanied by tail-flicking, and that tail-spreading was slightly less than half as common at intensity levels 2 and 3 of tail-flicking (21 observations) as at levels 0 and 1 (39 observations). Therefore, in all observations of tail-spreading taken together, there was a tendency toward a negative correlation between the occurrence of tail-spreading and the intensity of tail-flicking. But when the observations for specific calls are compared, it can be seen that the correlation is of a different nature with different calls. During Rattles, tail-flicking was rare, and 18 of the 19 records of tail-spreading occurred unaccompanied by tail-flicking. In contrast, during *Wah*'s low intensities of tail-flicking were rare, and all of the 13 records of tail-spreading occurred at relatively high intensities of tail-flicking. The tail-spreading during Rattles was with the tail motionless or depressed, while the tail-spreading during *Wah*'s was with upward flicks of the tail. Although the 13 observations of tail-spreading during the 79 *Wah*'s reported in table 7 are too few from which to draw conclusions, my general impression in the course of making hundreds of unrecorded observations was that tail-spreading during *Wah*'s was generally very rare at level 1 of tail-flicking and appeared only when the tail was being flicked at high intensities.

Thus there appeared to be two arbitrarily separable types of tail-spreading in respect to the integration of this activity with other behavior. One type was characterized by immobility or depression of the tail and was associated with a low crest angle, supplanting, threatening, Rattles, and, to a lesser extent, with *Shook*'s and a few other calls which were used in these contexts. The other type of tail-spreading was accompanied by a rapid raising of the tail and was associated with a high crest angle, mobbing, alarm situations, *Wah*'s, and other calls given during tail-flicking.

Since the occurrence of downward tail-spreading, such as accompanied Rattles, is physically incompatible with the occurrence of tail-flicking, a positive correlation of downward tail-spreading with crest angle might not be expected, in

view of the positive correlation, already demonstrated, between intensities of crest erection and tail-flicking (table 4). But table 15 shows that crest angles during Rattles averaged higher with tail-spreading (31 degrees) than without (17 degrees); and tables 14 and 7 show that tail-flicking, which might also be expected to influence crest angle, was rare during Rattles. Similarly, table 4, using a somewhat different set of data, shows that at intensity level 0 of tail-flicking the crest angle averaged lower at level 1 of tail-spreading (26 degrees) than at levels 2 and 3 of tail-spreading combined (46 degrees). At higher intensities of tail-flicking the data on upward tail-spreading were too few to be instructive.

Thus there appears to be a positive correlation between the occurrence and possibly the intensity of downward tail-spreading and crest angle. If a similar correlation is present for upward tail-spreading, it is masked by the more conspicuous correlation of crest angle and tail-flicking.

Tail-spreading was not commonly associated with Wing-spreading or Wing-flicking (tables 5 and 3). In 60 observations of tail-spreading, Wing-spreading occurred in 3 and Wing-flicking in 7. Tail-spreading occurred in only 3 of 46 observations of Wing-spreading, but in 7 of 22 observations of Wing-flicking. Generally, tail-spreading was associated with different behavioral contexts than were Wing-spreading and Wing-flicking (see the discussion of contexts for each of these activities), although the contexts of Wing-flicking and upward tail-spreading were similar.

CREST MOVEMENTS

CREST AS AN INDEX OF INTERNAL STATE

The crest of the Steller's jay may vary through a wide range of positions (fig. 11). Because these positions may be expressed in degrees of elevation of the crest, the variation in repeated observations of crest elevation for particular behavior patterns and comparisons between crest elevations for different behavior patterns may be dealt with quantitatively. Since observed differences in crest elevation were found to be correlated with certain types of behavior, it was a goal of this study to determine as accurately as possible the crest positions which accompanied a wide variety of behavior patterns. Such data make it possible to consider the extent to which variations in crest elevation are indicative of changes in the mood or behavioral predisposition of the bird.

COMPARISON OF CREST ANGLES IN VARIOUS ACTIVITIES

In order to evaluate the relation of crest angle to agonistic behavior, its relation to other types of behavior must also be considered.

Courtship.—The angle of the crest in every observed instance of courtship was low (fig. 3). Sidling and Circling were the principal components of the male courtship pattern, and they were occasionally used by females. In Circling, the male jumped slowly in semicircles or circles around the passive female at a distance of about a foot. In Sidling, the male perched parallel to the female a few inches away, then sidled slowly closer and could eventually mount her. During both of these acts the female remained perched and motionless. Since there was no detect-

able difference in crest angle between males and females in these acts, observations on the sexes have been combined. Courtship was observed many additional times when it was not possible to estimate the crest angle accurately, and in all of these the crest was also low.

Steller's jays remained paired and on their territories all year in the study area. Hence, most observations of courtship were on jays who were already paired. In the one certain and the few probable observations of pair formation, the same behavior patterns were used with the same crest angles, even when pair formation occurred in December—a time when courtship between already paired jays was not normally seen.

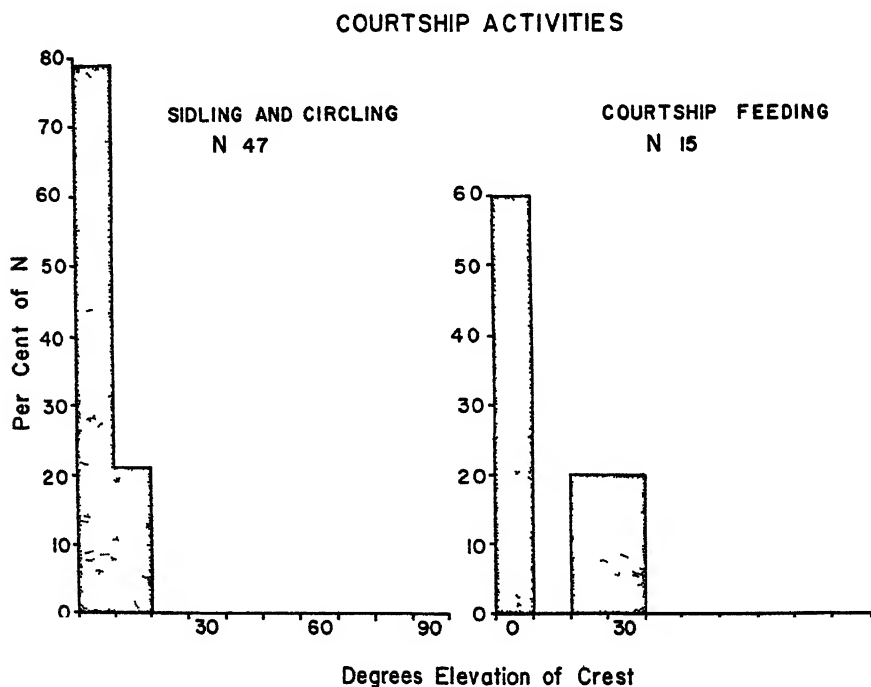


Fig. 3. Crest angles during courtship behavior of the Steller's jay.

In courtship feeding the male placed an item of food in the bill of the female. In all observations of courtship feeding the crest was low (fig. 3). Observations for males and females were combined. Whether courtship feeding had a real function as "courtship" does not matter for purposes of the present discussion, since it was not an exception to the generalization that the crest was not greatly erected during courtship of any kind in the Steller's jay.

Comfort activities.—The crest could be raised or lowered apparently independently of the feathers of the rest of the body. Generally, there was no correlation between the angle of the crest and erection of the body feathers. General feather erection over the body occurred mildly in preening and extremely during sun bathing. This general feather erection would account for the moderate crest angles observed during preening and the high angles during sun bathing (fig. 4). Crest

erection as a result of general feather erection occurred also during water bathing and when the jay was drying itself afterward.

During the performance of comfort acts the crest was raised in the absence of the agonistic contexts which accompanied crest raising at other times. Perhaps the most important point to be made regarding the crest during comfort activities is that the position of the crest could be controlled by more than one set of factors. In other words, the set of stimuli and internal states responsible for crest erection during sun bathing or preening was, as implied by striking qualitative differences in behavior and circumstances, qualitatively different from the set of stimuli and internal states which appeared to elicit the same degree of crest erection during aggressive encounters with other jays or in related contexts.

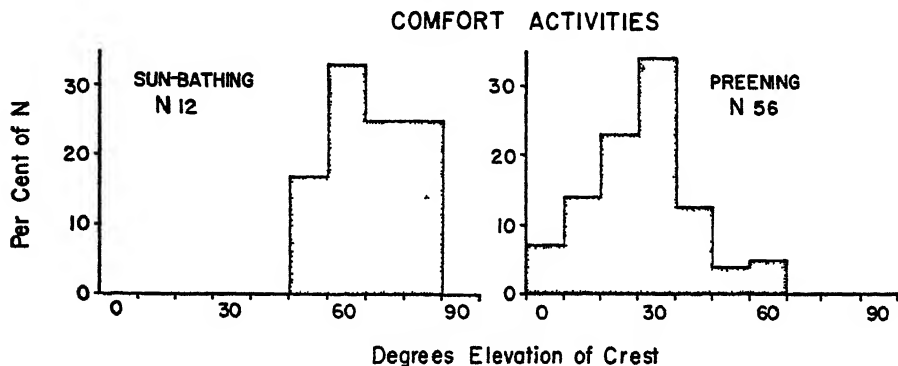


Fig. 4. Crest angles in some comfort activities of the Steller's jay.

Nutritive activities.—In all activities related primarily to the handling of food or drinking, the crest was usually low (fig. 5). High crest angles were sometimes observed during these activities, but they were rare. Differences in crest angle between different activities related to the handling of food were present, however. The crest positions accompanying the acts of storage, digging, and foraging, unlike those with the other nutritional activities as shown in figure 5, were characterized by a conspicuous mode at 0 degrees. In all of these the face was held close to the ground and the bill was frequently in contact with the ground. The observations of crest angle during the process of storage were made while the bill was inserted in the ground. Digging was accomplished by inserting the bill into the litter or earth and flicking the bill to one side together with a small quantity of litter. About two-thirds of the recorded observations of foraging were of birds on the ground but not digging; the others were all of birds foraging in oaks for acorns, on tree trunks, in old nests built by squirrels, on green leaves for caterpillars, or elsewhere in trees. In storage, the bill was fully inserted into the ground; in digging, less so; and in the other foraging acts recorded in figure 5, rarely. This sequence corresponds to the decreasing series of percentages of observations of the crest at 0 degrees in these activities: 85, 68, and 45 per cent respectively. This relationship suggests that something about the stimulus complex when the bill was in close contact with the substrate had a depressing action on the angle of the crest.

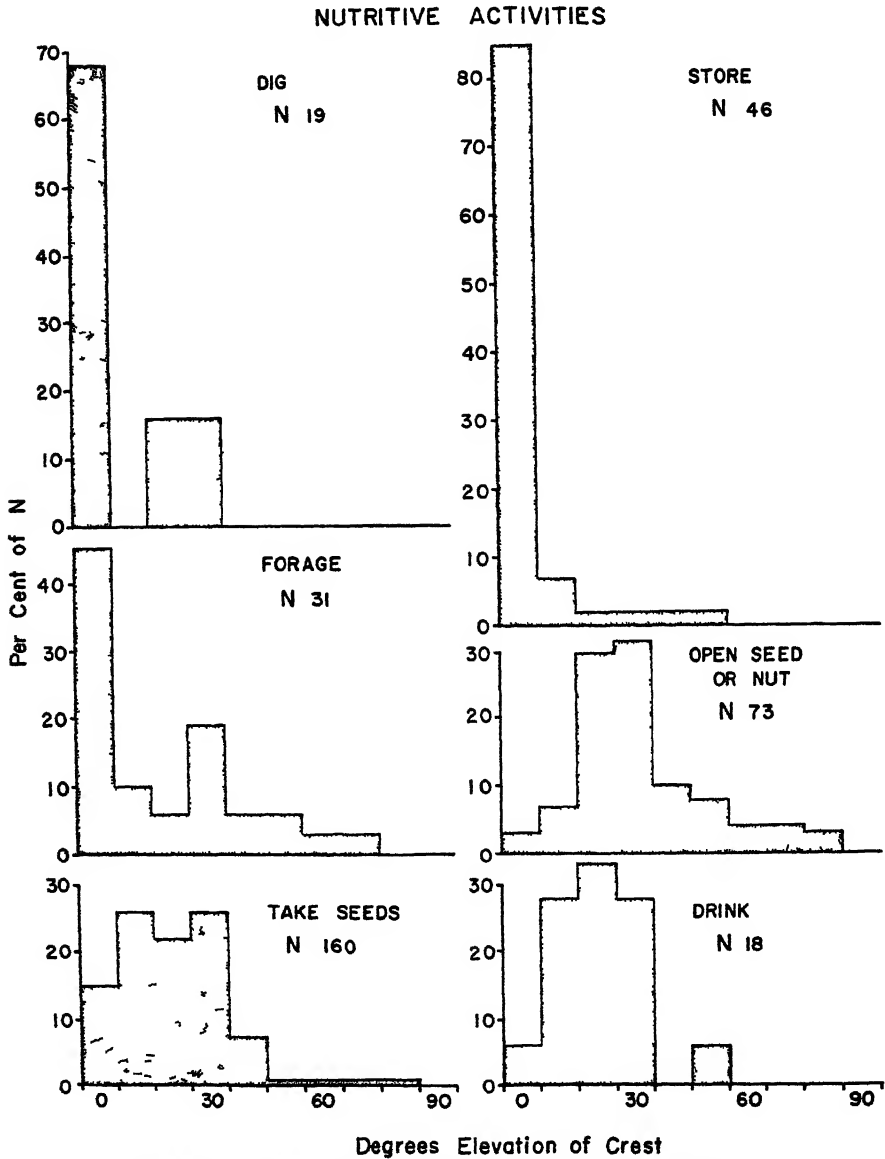


Fig. 5. Crest angles during nutritive behavior of the Steller's jay.

I received the same impression concerning individual jays engaged in the process of storing. In some, the crest was low during the whole procedure; but commonly when the jay first landed on the ground with an acorn or sunflower seeds in its bill, its crest was quite high. Then, just before or during the act of inserting its bill into the ground, its crest was quickly depressed. After withdrawal of the bill and covering up the storage site, the crest commonly rose again before the bird took flight.

In contrast to the activities discussed above, in which most of the observations

of the crest were at 0 degrees, the angle was quite variable while a jay was on a picnic table and taking into its mouth the sunflower seeds put out for bait. The angle in this situation ranged from 0 degrees to 40 degrees, rarely higher, and the distribution of angles showed no conspicuous mode at any particular angle. There appeared to be no mechanism which adjusted the crest angle for this particular situation. Instead, it appeared that a variety of factors were operating, and that the final crest angle was a resultant of their combined effects rather than primarily subject to the influence of one. When a jay landed on the picnic table its crest was frequently high. The crest usually went down gradually before or during the bird's approach to the sunflower seeds. Thus, the longer the time elapsed since landing, the lower the crest. In birds in their own territories undisturbed by other jays, the crest was usually low. In birds that had just arrived from a relatively distant territory, the crest often continued rather high at all times. Most birds, when first arriving from another territory, had high crests; but after several trips to the table their crests were lower and, in addition, they appeared less reactive to sudden disturbances. Familiarity with the area, the presence of other jays, the total time since their initial arrival, and the time since landing on the table all appeared to influence the crest angle in this situation.

The highest average level of crest erection during an activity related to feeding occurred during the hammering at, opening, and eating of nuts, sunflower seeds, or other relatively hard objects, for which activities the mode of crest erection was 30 degrees (fig. 5). This was probably also the most vigorous of activities related to food. In this more strenuous type of eating process, the whole body was raised and brought down strongly as the bill struck the object, which was held by the feet against the perch. Thus, the higher distribution of crest angles may be correlated with a higher level of physiological arousal accompanying the greater muscular exertion required in opening hard objects. Whether this is the explanation or not, the observations still indicate that this was another kind of situation in which stimuli influencing the crest angle were, so far as could be observed, qualitatively distinct from the social stimuli which influenced crest angle during aggressive contexts.

Agonistic behavior.—It was in agonistic behavior that the crest was most conspicuously employed. However, crest angle varied according to the nature of the agonistic behavior, in a complex fashion.

Combat.—The crest was most fully erected in actual combat. All of the observations of crest angles in combat recorded in figure 6 were of Steller's jays that were engaged in the most vigorous type of fighting with each other. In such situations, after the attack the two birds flew up 5 to 10 feet in close contact, with feathers flying, facing and pecking each other, and probably grasping at each other with their feet. The observations of crest angle were taken while the birds were in mid-air; hence, the number which I saw well enough to be sure of the crest angle was only 19; but in all of the other similar fights which I observed, the crest was in the neighborhood of 90 degrees.

Aggressive Sidling and displacement activities.—In Aggressive Sidling (fig. 6), the crest averaged almost as high as in fighting (fig. 6). Since many of the observations of displacement activities were made while the bird was engaged in Aggres-

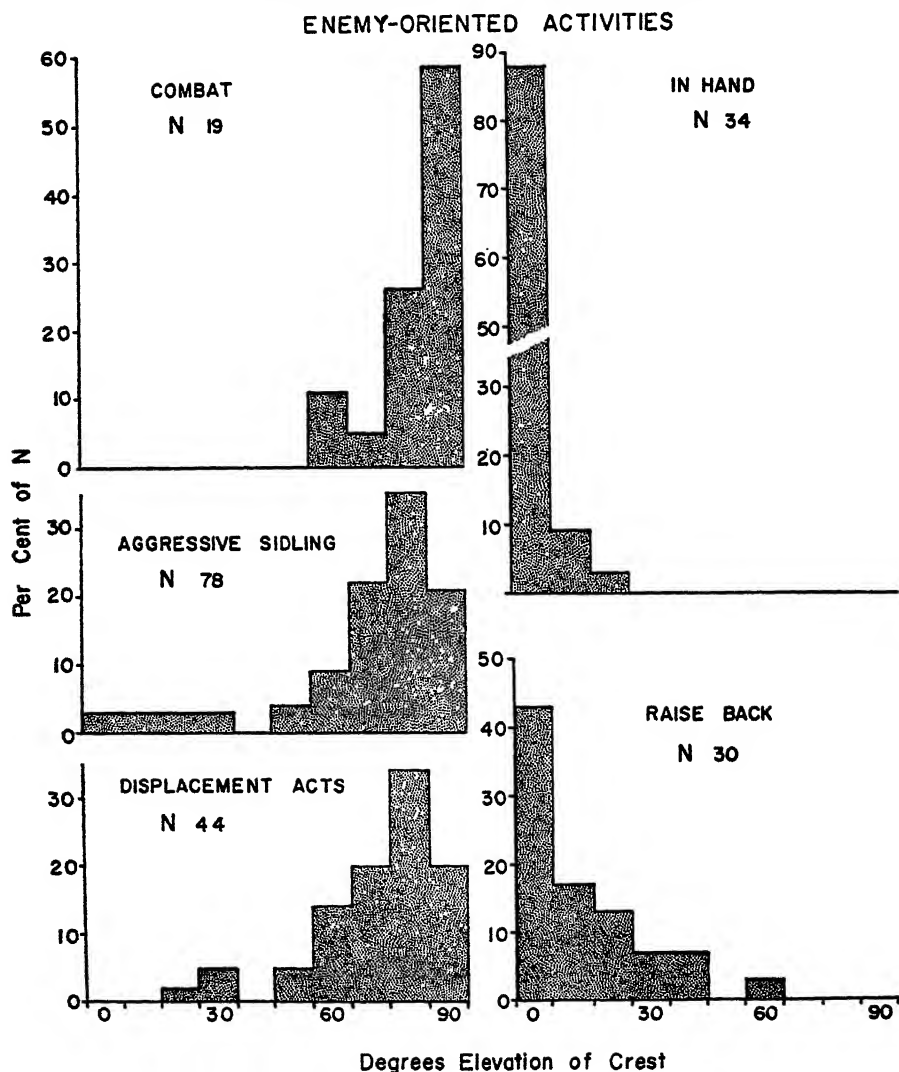


Fig. 6. Crest angles in agonistic behavior of the Steller's jay.

sive Sidling, the frequency distributions for these two categories of behavior are similar (fig. 6). The displacement activities for which crest angle was recorded were bill-rapping and displacement digging.

Attack NBM's and simple supplanting attack.—The high crest angles for combat and Aggressive Sidling suggest that an element of aggression involving a high probability of actual attack should be considered as a possible factor leading to erection of the crest. If crest erection were correlated simply with activity of attack NBM's, then it should also be prominent in supplanting attacks. Consequently, records were kept of the crest angle during the act of supplanting. It soon became evident that the relationship of the crest to supplanting was not simple. Therefore, in an effort to determine which factors were influential on crest angles,

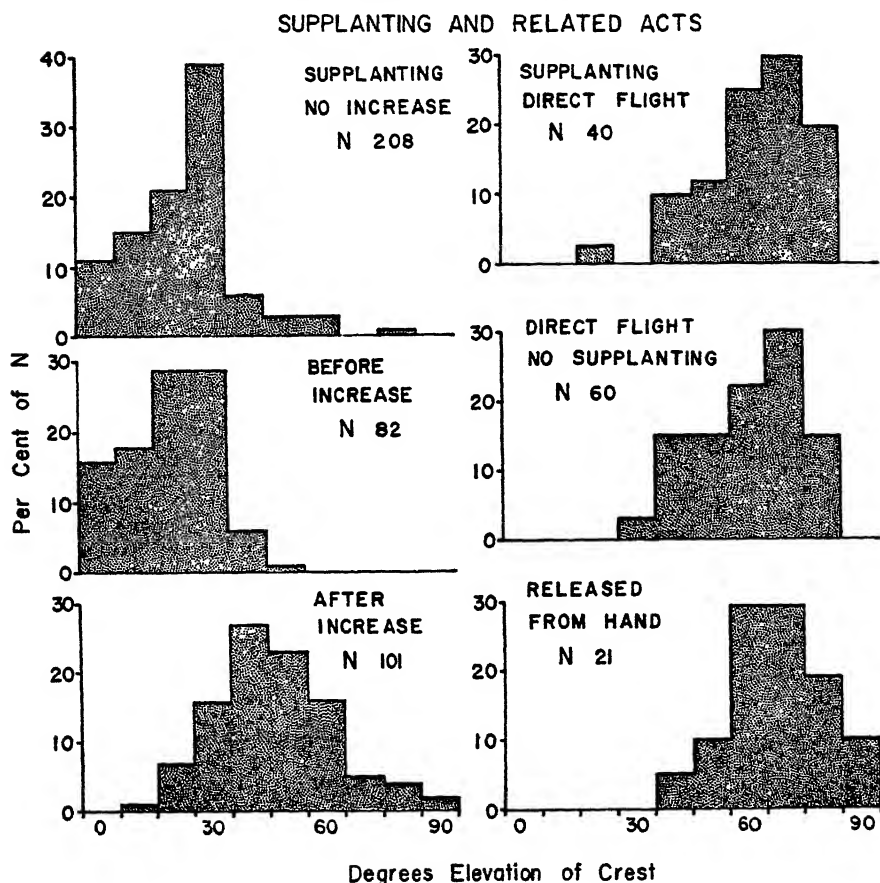


Fig. 7. Crest angles in the act of supplanting and related behavior in the Steller's jay.

I classified supplanting attacks according to whether the attack was made directly from the air or whether the supplanting bird began its attack from the table, and also according to the presence or absence of an increase in crest angle during the encounter.

All of the 349 observations of the crest angle in supplanting discussed here were made from November, 1959, through March, 1960, on jays which had been attracted to a pile of sunflower seeds placed on top of a picnic table. In order to eliminate variation that might be caused by differences in location, I made 75 per cent (261) of the observations at one table. Later, when it was found that no variation attributable to differences in location could be detected, observations of supplanting at other tables were added.

The simplest form of the activity was that in which the supplanting attack began on the table and there was no increase in crest angle. This was the most frequent type of aggressive encounter in the Steller's jay; 208 of the 349 supplantings were of this type. The frequency distribution of crest angles in this type of supplanting shown in figure 7 has a mode at the relatively low angle of 30 degrees. This indicates

that actual attacks were usually not accompanied by extreme crest erection. Therefore, the degree of crest erection was not correlated with the probability of actual attack even though the crest angle was greatest during fighting.

Correlation of sex and crest angle in supplanting.—Because the category of simple supplantings comprised the largest number of observations, the effects of sex and rank were investigated within it; the other categories were too small for these purposes. In table 23 observations of 10 males in 134 supplantings and 2 females in 37 supplantings are summarized. The females are listed individually because they were markedly different. Female MVM-VXM behaved consistently in an unusual manner; she would raise the feathers of her back and depress her crest in situations in which other jays would have been expected to raise their

TABLE 8

CREST ANGLE IN THE STELLER'S JAY IMMEDIATELY AFTER THE BIRD HAS BEEN SUPPLANTED

Situation	Degrees of elevation of crest											Mean
	0	10	20	30	40	50	60	70	80	90	N	
In supplan- tee.			1	3	4	13	14	8	2	1	46	56

NOTE: The number of observations at each crest angle and the mean crest angle are listed.

crests. Consequently, most of her records are at 0 and 10 degrees. Female XW-WW, by contrast, represented the typical female and was the dominant female at the table where most of the observations were taken. Her records show a mode at 30 degrees, with the second greatest number of observations at 20 degrees—a distribution similar to that of the 10 males. Hence, there appeared to be no important difference in crest angle between males and females in simple supplantings; however, data on additional individual females would be desirable for the purpose of substantiating this statement. Similarly, Boyd (1953:116) was unable to demonstrate a clear difference between the sexes in intensity of threat in encounters between wild white-fronted geese (*Anser albifrons*) on the wintering grounds.

Relation to rank in dominance hierarchy.—On the basis of 637 observations of supplanting encounters at one picnic table from November, 1959, through March, 1960, a dominance hierarchy of the straight-line type was recorded among jays that were almost all paired residents. The mean crest angles of individuals that were attacking in relation to their rank in the hierarchy is shown in table 9. No significant relationship between rank and crest angle is apparent.

Because crest angle in supplanting was correlated with the resistance of the opponent (see below), it might be expected to be correlated also with the rank of the opponent in the dominance hierarchy, since high-ranking opponents would offer more resistance. If so, it should be higher against higher-ranking opponents. In table 10 a comparison is made between the distributions of crest angles in supplantings over the top 5 subordinates in rank beneath a given individual, and supplantings over the subordinates which ranked beneath these top 5. The data represent the pooled records for nine individuals in the hierarchy. The crest angle was greater against higher-ranking subordinates, but the difference between

the two groups is not statistically significant ($P > 0.01$, $P > 0.01$, $P = 1.0$, using a t test) in any case. The mean crest angles were higher against high-ranking subordinates than against low-ranking ones in 4 individuals, but lower in 3. Therefore, using these criteria and data, no clear correlation of crest angle with rank of opponent is detectable. Similarly, in white-fronted geese, Boyd (1953), using data from 549 encounters, was unable to find "a connection between threat-intensity and status of the victim."

Supplantings with an increase in crest angle.—In some supplanting attacks which were begun on the picnic table there was a conspicuous increase in the erection of the crest of the attacker. Such increases occurred primarily when the subordinate was slow in leaving, if it were taken by surprise, or if it attempted

TABLE 9
MEAN CREST ANGLES OF SUPPLANTING JAYS IN RELATION TO THE INDIVIDUALS' RANK
IN THE DOMINANCE HIERARCHY AT ONE PICNIC TABLE

Statistics	X-YY	VR-RR	XY-OO	YRY-X	O-RXR	XW-WW	All individuals
Rank in hierarchy...	1	2	3	4	5	9	..
Mean.....	26	25	28	23	31	30	26
N.....	39	13	24	26	14	26	171

NOTE: Records are for encounters in which no increase in angle occurred during simple supplanting attacks begun from the table top. The mode for all individuals except VR-RR was 30 degrees; all are males except female XW-WW. The table where the observations were made was within the territory of the mated pair X-YY and XW-WW. The other four males were paired and held territories adjacent to that of X-YY.

to resist the dominant jay. Generally, when the subordinate bird allowed the dominant one immediate and uncontested access to the seeds, there was no increase in crest angle in the dominant; and there was even a slight decrease occasionally. The encounters in which increases occurred began with crest angles similar to those in which no increases occurred, as illustrated in figure 7, but they culminated with an increase in mean crest angle from 20 degrees to 46 degrees. The amount of increase in individual cases ranged from 10 degrees to 30 degrees generally, and rarely to 40 degrees. When greater increases occurred, the encounter could usually not be classed as supplanting, but developed into Aggressive Sidling or actual fighting.

Agonistic arousal.—When the frequency distributions of crest angles for many diverse activities are compared, the possibility that the angle of the crest is completely or primarily controlled by the activity of a unitary central nervous mechanism or "drive center" seems remote. Evidence has already been presented to show that the integrative systems controlling crest angle in the activities of storage, preening, and opening hard objects differ from each other and from other systems affecting crest angle. It seems probable, therefore, that diverse sets of stimuli may act through diverse central integrative systems to control crest angle, especially in the lower range of angles. If the observations on agonistic behavior discussed above are considered together, another and perhaps the most important integrative system controlling crest angle may be postulated.

The behavior of a dominant jay in or near its territory in relation to varying

amounts of opposition by another jay is considered in table 11. When no opposition was observed, such as in foraging, digging, courtship, resting, and some other activities, the crest angle was usually near 0 degrees. When there was an opponent which offered little or no resistance, the modal crest angle was 30 degrees. When the opponent offered moderate or brief resistance but was still quickly vanquished, the modal crest angle was 40 degrees. And when the opponent refused to leave, the modal crest angles were 80 degrees during Aggressive Sidling and 90 degrees during actual fighting. Thus we find that a positive correlation exists between the observed degree of resistance of an opponent and the quantitative estimates of crest angle. This is a correlation between strength of stimulus (resistance) and

TABLE 10
CREST ANGLES OF SUPPLANTING JAYS IN RELATION TO RANK OF THEIR OPPONENTS
IN THE DOMINANCE HIERARCHY AT ONE PICNIC TABLE

Category	0	10	20	30	40	50	60	70	80	90	N	M
No increase in angle:												
Over top 5 subordinates.....	5	3	11	32	7	4	4	1	67	30
Over subordinates below top 5....	2	15	27	34	5	2	3	..	1	..	89	26
Peak angle after increase:												
Over top 5 subordinates.....	4	2	8	9	6	4	3	..	36	50
Over subordinates below top 5....	2	8	10	10	3	1	34	42
Before increase in angle:												
Over top 5 subordinates.....	5	4	7	12	3	1	32	22
Over subordinates below top 5....	1	5	12	9	2	29	22

NOTE: Records are for simple supplanting attacks begun from the table top.

intensity of response (crest erection), but it implies corresponding differences in the activity level of a complex of intervening variables which constitute the central nervous integrative system for agonistic behavior.

Although direct experiments on the postulated central nervous integrative system for crest erection in aggressive encounters have not been made in the Steller's jay, to circumscribe some of its properties by considering the relationships between observed types of agonistic behavior is desirable. Accompanying the series of behavior patterns in table 11, from foraging to fighting, are probable changes in a number of physiological variables, such as blood pressure, heart rate, heat production, blood sugar, muscular effort, and activity in the areas of the central nervous system (CNS) which control these variables. The same sequence of behavior patterns is characterized by the increasing frequency and intensity of vocalizations and by the increasing duration and intensity of complex muscular exertion. Collectively these physiological and behavioral changes may be interpreted as reflecting increasing levels of central nervous arousal. Since the behavior was oriented toward rival jays and since it employed behavior patterns generally restricted to agonistic contexts, the series will be referred to as one of increasing levels of agonistic arousal. (See the discussion below, in the section entitled Integration of Agonistic Behavior.)

Alighting and alarm contexts.—The sequence of agonistic behavior patterns just

considered, with the exception of combat, was restricted generally to activities which occurred after a jay had been perched for a significant length of time. Complications are added when we consider the situations in which a jay had just landed from a flight of about 15 feet or more. When supplanting was accomplished by a direct flight to the seeds and the supplanting bird landed at the same spot formerly occupied by the subordinate, the modal crest angle of the supplanting bird was much higher than in other supplanting attacks (see Supplanting by direct flight, in fig. 7), despite the fact that there was little or no resistance by the opponent. The act of landing on the table seemed to be the principal difference correlated with the higher crest angle. To test this hypothesis, I made observations

TABLE 11

A COMPARISON OF ACTIVITIES IN A DOMINANT STELLER'S JAY IN RELATION TO ITS CREST ANGLE AND THE RESISTANCE OF ITS OPPONENT

Activity	Resistance of opponent	Postulated agonistic arousal	Modal crest angle
Foraging.....	None	Slight	0°
Supplanting:			
No increase in crest angle.....	Slight if any	Slight	30°
Increase in crest angle.....	Moderate	Moderate	40°
Aggressive Sidling.....	High	High	80°
Combat.....	Extreme	Extreme	90°

NOTE: Crest angle in the dominant bird increases with increasing resistance of the opponent.

of crest angles in jays which had landed on a table immediately before the incident recorded, but which were not in any way involved in the act of supplanting. Of these 60 observations, 47 were of jays landing alone on the table, and 13 were of jays landing where other jays were present; but no difference in crest angle could be detected between these two groups. The frequency distribution of crest angles (Direct flight, no supplanting, in fig. 7) was very much like that for supplanting by direct flight. The lack of a detectable difference in crest-angle distribution between the situations "landing alone" and "landing with supplanting" suggests that the high crest angles during direct supplanting were correlated primarily with the fact of having recently landed on the table, rather than with the act of supplanting.

The high crest angles in these situations could not safely be attributed to the act of alighting alone, for jays commonly alighted with low crests in other contexts. Rather, the condition of arriving suddenly at an exposed site subject to intrusion by man, to aggressive encounters with other jays, and often outside the jay's own territory, could be related to the appearance of nervousness in the jay. Jays with their crests high just after alighting reacted to slight noises and disturbances of the sort which they would normally have ignored, by flying immediately for cover. Or they frequently leaped 3 to 4 feet into the air from the table at very slight disturbances. After landing, the jays often paused before going to the seeds. During this pause and while a jay was approaching and

taking the seeds, crest erection usually declined fairly rapidly if the jay was familiar with the surroundings, or very little if the area was one in which the bird was infrequently observed. Jays coming to the seeds in their own territories for the first time on a particular day normally landed with crest erect and gave the *Wah* call a few times. But after one or two more trips to the table most further landings on the table were made with the crest low, as long as the territory owners were alone. When other jays arrived the situation became more complex, and the crest was sometimes erected to a greater extent.

Obviously, a great variety of factors influenced the extent to which a jay was "at ease" or "alert" at a particular table, and no attempt was made to separate these factors quantitatively. Jays high in the dominance hierarchy seemed to become "confident" more rapidly than did the lower-ranking jays. A wind rustling the eucalyptus leaves and blowing loose leaves through the area seemed to facilitate a jay's appearance of alertness and high reactivity. Other factors already mentioned included the length of time since alighting, the number of trips to the table, and distance from the bird's own territory. Individual variation appeared important, also. Some individuals (e.g., female XWW-RGW) almost invariably had their crests erect when they were on picnic tables, in contrast to others (e.g., female MVM-VXM) who rarely did, although these two types were comparable in respect to distance from their own territories and to dominance rank.

All of the factors mentioned above have in common the feature that they relate to the jay's safety. The crest erection, high reactivity to slight disturbances, and the calls sometimes given in such contexts may, therefore, be considered danger-oriented or agonistic behavior. And so the high crest angles seen immediately after alighting may be correlated with a high level of the postulated intervening variable of agonistic arousal.

A distribution of crest angles similar to those for alighting with or without supplanting was obtained for jays who had flown to a perch immediately after being released after banding (see Released from hand, in fig. 7). Having just "escaped" from the hands of a "predator," these jays no longer had the depressed crest characteristic of jays in the hand; but they had high crests, frequently called loudly, and flicked their tails vigorously and sometimes their wings, with much the same behavior as jays mobbing an owl. Thus they could be said to show a high level of agonistic arousal. There was no reason for them to be any more afraid after release than when held in the hand with depressed crest; therefore, the erection of the crest in such situations might easily have been correlated not with an increase in fear, but with a decrease.

Jays which had been supplanted would jump a few feet or fly a short distance or out of sight. In 44 of 47 jays whose crests were watched while and after the birds were being supplanted, there was a conspicuous increase in crest angle; in 3 there was no change; and in none was there a decrease. The frequency distribution of crest angles for these birds also resembles those for alarm contexts in which jays have alighted in a situation characterized by potential danger to the jay and a probable high level of agonistic arousal (compare table 8 with fig. 7).

When a jay alighted after being supplanted, its tail was often flicked vigorously and its crest was high. If the jay remained, the tail-flicking usually decreased rapidly in intensity and the crest erection also decreased. Jays observed flicking their tails vigorously had crest angles similar to those in situations, discussed above, in which jays had just alighted; and, in fact, most of the jays showing vigorous tail-flicking had recently alighted. Weak tail-flicking was correlated with a lower average crest angle.

Erection of feathers on back.—The feathers of the back were rarely erected, but when erection occurred it was in aggressive encounters in which some resistance was shown by the opponent. Therefore the finding that the crest was usually actively depressed in these encounters, often to 0 degrees, was unexpected (fig. 6). It is an exception to the generalization that increased resistance stimulates a higher crest angle.

Most of the observations were of females, and 24 of the 30 observations on which the distribution in figure 6 is based were made on 1 female, MVM-VXM. The display was seen in only 2 other females and 3 males. MVM-VXM ranked near the bottom of the dominance hierarchy at the places where most of the observations were made; but she was rebellious occasionally and would then display her humped back at jays that would normally dominate her. On 2 occasions she was successful in bluffing a hesitant scrub jay in this manner; but on at least 2 other occasions when she displayed at other Steller's jays, she was attacked and driven away after an initial hesitation by the dominant jay. The typical lack of a high level of agonistic arousal during this display is suggested not only by the crest-angle distribution but also by the rarity of calls during the display (see the subsection above, under the heading Raising of the Back).

One possible explanation of the occurrence of this display only in certain individuals might be that in agonistic contacts certain jays, such as MVM-VXM, were genetically predisposed to erect the back rather than the crest more often than were other individuals in similar situations. However, at other times MVM-VXM was commonly observed with erect crest. Another possibility is that the display was dependent on combinations of stimuli and internal states which occurred only rarely. If this were true, MVM-VXM may have been predisposed toward these combinations by genetic or other factors. The virtually complete absence of this display in dominant males and its occurrence in MVM-VXM, a subordinate but rebellious female, suggest that resistance to a feared opponent was an important aspect of the situation which elicited the display. The crest was also depressed in two other contexts associated with fear, that of wild-caught jays attempting to hide from people in an aviary, and that of jays held in the hand while being banded.

VOCALIZATIONS

Unlike many passerines, the jays, and the Corvidae generally, are not noted for their songs. They are known best for their loud and often harsh calls, which in the Steller's jay form the predominant elements of the vocabulary. It should not be expected, then, that the employment of the voice by jays would follow the

pattern of more typical passerines. Instead, the various functions which song has in other passerines seem to be divided among several different calls and the so-called "Song" in the Steller's jay.

SONG

FORM

The Song of the Steller's jay was the only one of its vocalizations that sometimes continued for several seconds uninterrupted by pauses and was even continued for minutes at a time with but slight breaks. It was invariably of a low amplitude and was almost inaudible to the human ear beyond 75 feet from the

TABLE 12
SEASONAL VARIATION IN FREQUENCY OF TEE-AR'S AND TOO-LEET'S AT INDIAN CAMP

Subject	1959										1960			
	M	A	M	J	J	A	S	O	N	D	J	F	M	A
<i>Tee-ar's</i> /10 hours.....	65	50	24	19	19	51	42	46	14	8	26	55	35	26
<i>Too-leet's</i> /10 hours.....	14	25	6	7	5	3	8	4	+	5	1	5	6	8
Hours in field.....	26	48	50	45	30	26	28	26	28	28	24	29	35	20
Per cent of days, <i>Tee-ar's</i> ...	90	78	65	79	92	92	100	100	77	67	80	92	100	78
Per cent of days, <i>Too-leet's</i> ..	90	94	60	42	62	42	50	8	8	50	10	50	54	78
Days in field.	10	18	20	19	13	12	12	12	13	12	10	12	13	9

NOTE: All observations were made in the morning, generally in periods of at least two hours' duration per day. Each *Tee-ar* call and each series of *Too-leet's* heard in the study area were counted. The observations for each month have been summed and divided by the number of hours spent in the field for that month, to give an index of the frequency of *Tee-ar's* and *Too-leet's*. The seasonal distribution of some other calls are shown in figure 1.

performer. No stereotyped pattern was evident in the Song; rather, it consisted of a series of whistled, harsh, or gurgled notes and popping or snapping sounds run together and with frequent repetitions, a vocalization suggesting the songs of some members of the Mimidae, except for its soft quality. It was much like the songs of the scrub and Mexican jays and resembled published descriptions of the song of the blue jay.

POSTURE

The partner which took the active role in Sexual Sidling and Circling (courtship), almost always the male, was often observed to be singing at the same time. Here the posture of the bird was no different from the postures involved in Sidling and Circling, except that the bill was open several millimeters and the throat was moving. When the female was not present, however, a singing jay could often be recognized by its characteristic posture and actions, even though the bird was too far away for the Song to be heard. The Song was then given in a posture typical of a jay resting on a perch, with its tail and body in line and not far from vertical. The head was very slightly extended forward and was turned slowly from side to side through an arc of about 200 degrees. This gave an additional ventriloquial quality to the Song; and it was indeed difficult to locate a singing jay by sound. The extent to which the bill was open varied

slightly in the course of the Song. The crest was typically depressed during singing (fig. 8). The tail could be vibrated back and forth through an arc of 5-15 degrees, but this was uncommon.

CONTEXTS

Seasonal frequency.—Songs were recorded in every month except November and January, but they were most frequent from March through September.

Sex and age.—Although Song was most often heard from mated males and less often from mated females, unmated jays of both sexes not possessing territories

TABLE 13

INDIVIDUAL DIFFERENCES IN FREQUENCY OF USE OF SOME VARIATIONS OF THE MUSICAL CALL
AMONG RESIDENT MALE STELLER'S JAYS AT INDIAN CAMP

Individual	Variation of the Musical call		
	<i>Toodles-oot</i>	<i>High oot</i>	<i>Low woot</i>
X-YY.....	Common	Rare	Absent
O-RXR.....	Rare	Common	Absent
YRY-X.....	Common	Common	Absent
XY-OO.....	Absent	Rare	Common

were sometimes observed singing. Jays in their first autumn were also observed singing during or after periods of rest, but these Songs tended to be louder than those of adults and included a variety of other calls in imperfect form; hence, they were not entirely typical.

Solitary jays and courting jays.—The Song was commonly given by males who were Sidling or Circling a female in courtship. Rarely a female sang while being courted by a male, or she sang while Circling a male.

The principal function of singing would appear to be in connection with courtship; however, singing was observed as often in jays which were essentially alone as in those engaged in courtship. In many, but not all, of these cases of Song given by isolated jays, it appeared to be stimulated, at least in part, by the proximity of the observer. Not uncommonly, elements of appetitive behavior for the consummatory acts, incompatible in these cases, of feeding and avoidance of the observer were present at the same time in singing jays. For instance, when a lone jay which had been foraging noticed the observer about 25 feet away, it would begin to sing and either continue foraging while watching the observer at the same time if in a tree, or would wait and resume foraging after he had left. Jays during such situations did not appear "jumpy" or aroused, but perched or moved about unhurriedly and inconspicuously. That jays were almost invariably in high and rather dense cover when singing may have had some effect in preventing a higher level of arousal, since they probably felt more secure with such protection.

Song was not observed to be connected with territorial defense in any way, and thus differed from most of the other calls, which could be so employed.

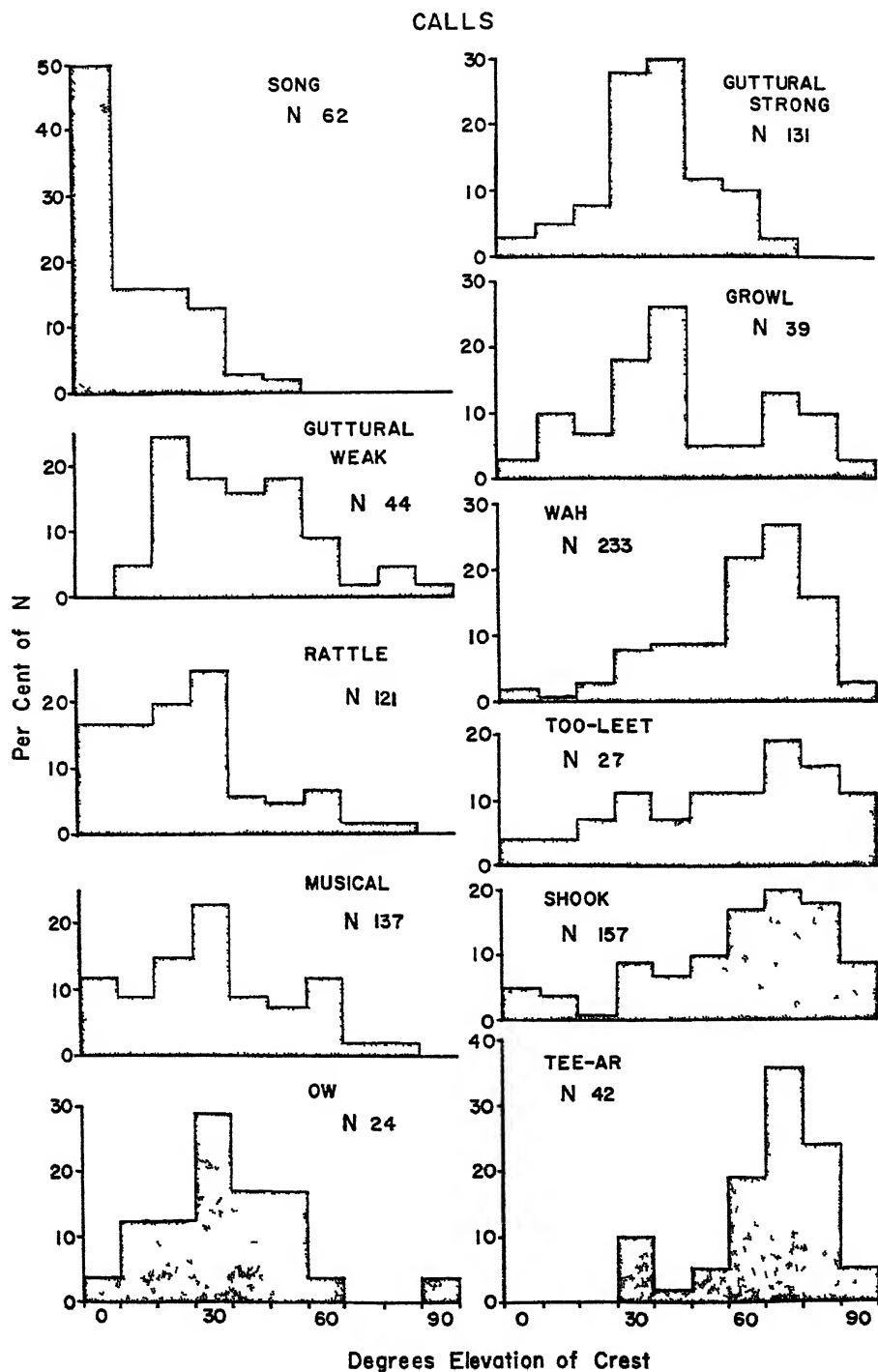


Fig. 8. Crest angles in vocalizations of the Steller's jay.

INTEGRATION WITH OTHER BEHAVIOR

Song as a displacement activity.—Song under similar circumstances in the gray jay (*Perisoreus canadensis*) has been interpreted as a displacement activity (Lawrence, 1957). If Song in the Steller's jay is regarded as a sexual act because of its association with courtship, then Song in lone jays mildly disturbed or frustrated by a person nearby would be functionally irrelevant and might qualify as a displacement activity despite the lack of some of the other characteristics of displacement activities. If, however, Song is not specifically integrated with the pattern of behavior during courtship, but instead indicates a particular state of mild arousal which happened to be common during courtship but also at other times, then its designation as a displacement activity would be misleading. Since the evidence at hand is insufficient to permit me to distinguish between these two alternatives, Song is not here recognized as a displacement act in the Steller's jay. The low level of arousal that is characteristic of a singing jay is inconsistent with the high level characteristic of displacement activities in this and other species. Furthermore, the stereotyped head turning which accompanies nonsexual singing in the Steller's, scrub, and Mexican jays argues against the theory that Song may be a displacement activity.

Arousal and attack and escape NBM's.—That Song was correlated with a low level of general bodily arousal is suggested by the frequency with which it followed periods of resting, preening, and stretching, and by the relative inactivity of singing jays. Jays which had been resting for several minutes during the day, if approached gradually by the observer, often sang if they had not been alarmed by sudden disturbances. Then, after the usual stretching and preening which followed a rest, they resumed normal activity.

Singing was never followed by attacks or escapes without a marked change in the social environment, nor did it occur in contexts which were agonistic to an extent greater than is indicated above. It was, however, associated with a hesitancy to approach, which might be interpreted as resulting from low level activity of the NBM's for escape.

GUTTURAL NOTES

FORM

There was not just one type of Guttural note; instead, there were many types, with all degrees of intergradation. These could sound quite different from one another, but since they intergraded so frequently they will be discussed together. They may be referred to as *ut*'s at low intensities, and as *aap*'s or *amp*'s at high intensities. Part of the difference in sound between these types seemed to be correlated with the extent to which the bill was opened during the call. If it was barely open, the call had a muffled quality sounding like "*ut*" or "*up*." But if the bill was wide open, the call was louder and sounded more like "*aap*."

POSTURE

A jay could give Guttural notes in a wide range of intensities with no variation from its normal perching postures. However, especially at higher intensities,

Gutturals were usually associated with Wing-spreading, which has already been described. Some degree of Wing-spreading probably occurred on about half of the occasions when Gutturals were given, although the frequency was largely dependent on the social context of the call.

The distributions of crest angles during the utterance of Gutturals accompanying Weak (0 and 1) and Strong (2 and 3) intensities of Wing-spreading are shown in figure 8; it may be seen that the modes during Weak and Strong Wing-spreading are 20 degrees and 40 degrees respectively; however, because of the wide variation in crest angle during Gutturals unaccompanied by Wing-spreading, the mean crest angles are not significantly different, being 39 degrees for Weak Gutturals and 37 degrees for Strong Gutturals.

CONTEXTS

Since Guttural notes, or sometimes *Ow*'s always accompanied Wing-spreading, the contexts in which they occurred have been discussed in connection with those calls. Situations in which the Guttural notes were not accompanied by Wing-spreading were generally similar, but the stimuli and motivational states accompanying them were less intense.

One exception is a variation with a more nasal quality, referred to as *amp*, which has been observed in Aggressive Sidling. It was usually given loudly but without any Wing-spreading and with a relatively high crest angle; this variation accounts for some of the high crest angles during Weak Gutturals noted in figure 8.

In summary, Guttural notes given by both sexes were common throughout the year, but most common during the preincubation phase in association with courtship feeding, nest building, courtship, boundary disputes, and related activities.

RATTLE

The Rattle was a common call of females, and was never observed to be given by a jay known to be a male (see also table 2). Both mated and unmated birds gave the call, but especially the former.

FORM

Often the Rattle was preceded by an accelerated series of low Guttural notes unaccompanied by Wing-spreading. In quality the Rattle was unlike any other call of the Steller's jay. It had a mechanical or rolling quality similar to that obtained by vibrating one's tongue against the roof of one's mouth, or drawing a fingernail along the teeth of a comb. It lasted from one-half of a second to almost two seconds or longer, and was virtually all on the same pitch. Although similar in sound to the Rattle of the scrub jay, it usually differed in having a change in tone quality from a long "o" sound to an "ee" sound about midway through the call; the change was associated with the gradual opening of the bill at this time. The two-toned effect was absent in some juvenile Rattles, or sometimes when a Rattle was cut short during the act of supplanting, but was almost always present. During the rattle of the scrub jay, the bill was kept in one position throughout the performance. Since in the Steller's jay the Rattle was the

principal call given only by females and was given during the early stages of pair formation, this difference in tone quality might have significance as a behavioral isolating mechanism.

POSTURE

The Rattle of the Steller's jay was not accompanied by a stereotyped display, as it always was in the scrub jay. It was frequently given when the bird was in a normal perching or standing position, less often in flapping flight or when the

TABLE 14
EMPLOYMENT OF TAIL AND WINGS DURING VOCALIZATIONS OF THE STELLER'S JAY

Vocalization	Tail-flicking					Tail-spreading					Wing-flicking		
	0	1	2	3	N	0	1	2	3	N	0	1-4	N
Guttural.....	67	13	9	8	97	90	6	96
Rattle.....	44	2	46	28	15	6	5	54	47	..	47
Musical.....	34	..	2	..	36	36	..	1	1	38	36	1	37
Growl.....	6	3	2	2	13	10	3	13	8	4	12
Wah.....	9	5	33	48	95	68	11	1	2	82	73	12	85
Too-leet.....	7	1	8	5	..	1	..	6	6	1	7
Shook.....	21	3	2	3	29	23	3	2	2	30	36	..	36
Tee-ar.....	6	6	1	1	14	11	1	1	..	13	15	1	16

NOTE: Data were collected while investigator was recording crest angles. The numbers of occasions on which each act was noted are listed under four arbitrary levels of intensity, which are explained under table 4.

TABLE 15
DISTRIBUTION OF CREST ANGLES DURING RATTLES WITH AND WITHOUT SPREADING OF THE TAIL

Category	0	10	20	30	40	50	60	70	80	90	N	Mean
Without tail spreading.....	8	8	5	4	0	1	2	28	17
With tail-spreading.....	..	3	6	11	3	1	2	0	1	..	27	31

NOTE: Data are in actual numbers of observations.

jay was gliding with spread wings and tail. The head and neck were sometimes slightly extended, with the bill as much as 45 degrees above horizontal.

On 55 occasions when Rattles were observed, the tail was spread to a varying extent in 27 and was kept folded in 28 (tables 14 and 15). The tail was conspicuously but usually not fully spread at these times. This indicates that the tail was frequently spread during the Rattle, but should not be interpreted as an accurate estimate of the frequency of tail-spreading during the Rattle. The tail was only rarely if ever flicked during a Rattle, nor were the wings flicked (table 14). The distribution of all crest angles recorded during Rattles may be seen in figure 8, which shows that in almost 80 per cent of the observations the crest was at 30 degrees or less. Therefore, the crest was typically rather low during the Rattle. The crest angle averaged higher when the Rattle was accompanied by tail-spreading than when not (table 15).

During a Rattle given in an aggressive context the crest usually did not

change in elevation. But if the Rattle was given just after the bird had landed on a table, the crest sometimes declined in elevation during the Rattle as it normally would in the same situation if the jay was silent. Also, since the crest was often raised in a supplanting attack when resistance was encountered, the crest was sometimes raised during a Rattle given in such a situation.

On some occasions, however, there was a rapid depression of the crest at the inception of a Rattle and an immediate elevation at its cessation which could not be correlated either with recent landing or with resistance in the course of an attempt to supplant. For example, the crest angle could go from 30 degrees to 0 degrees while the Rattle was being given and then back up to 30 degrees afterward. It was not possible to correlate this action of the crest in the course of a Rattle with a particular behavioral context. Rather, it appeared to be characteristic of the Rattle when not masked by other behavior. In these instances it seemed improbable that a significant physiological change occurred at the inception and cessation of the Rattle; therefore, the depression and elevation of the crest during the Rattle would not appear to be correlated with the general autonomic changes which might be expected to accompany changes in crest elevation at some other times.

CONTEXTS

Seasonal frequency.—The seasonal increases and decreases in frequency of Rattles heard in the field are indicated in figure 1. Rattles were heard in every month of the year, but were particularly common during the preincubation stage, from February to April. Days in which they were not heard were most numerous in the cooler months, from October through January.

Agonistic situations.—Table 19 records the contexts of 49 Rattles. I made the observations while recording crest angles, and did not collect the data in such a way that they would indicate accurately the distribution of Rattles according to contexts. But they do illustrate the fact that most adult Rattles (41 to 49) were given by jays in aggressive contexts, usually either in connection with supplanting (27) or as a threat toward particular individuals (12). In supplanting, the victor gave the Rattle far more often than the vanquished, 25 versus 2 observations respectively.

It was found that in aggressive encounters between two jays the Rattle was the most commonly used call by females. Table 17 shows that 74 of the calls used by 8 females in 107 of such situations were Rattles. These situations usually involved encounters between two jays when there were no other jays nearby. In cases in which encounters in groups or between pairs occurred, Guttural notes seemed more common than Rattles.

Of the jays who elicited the Rattles in these instances, 83 per cent of 60 jays of known sex were females. This is not surprising, since the Rattle was usually given by the dominant female in an encounter, and since most of the jays subordinate to a female were also females, as shown by parallel studies of dominance hierarchies. Therefore, femaleness as such may or may not have been a less important factor than rank in the dominance hierarchy in eliciting Rattles.

In respect to the female for which the most records were available, XW-WW,

it was found that the neighboring female (MO-MXV) on one side of her territory elicited more Rattles than any other individual (15 of a total of 39). And the second highest number of Rattles (5) at a known individual was elicited by the neighboring female (XMR-RMY) on the opposite side of XW-WW's territory. The other 4 females and 8 males which elicited Rattles from XW-WW were all paired adults with territories not far away.

Localization in respect to territory.—Rattles were most frequently given within or near the border zone of the territory. Less often, they were given quite far outside the territory, as sometimes in courtship. Two of the factors which may have accounted for the greater frequency of Rattles within the caller's territory were (1) the greater amount of time spent there and (2) the higher rank in the dominance hierarchy which obtained there for the female concerned.

Situations eliciting Rattles.—As has already been indicated, Rattles were often employed in situations in which aggressive competition occurred between jays. On many of the occasions discussed above (at least 55) the jays were competing for sunflower seeds placed as bait on picnic tables. On these occasions it was usually the territory owner who Rattled. Frequently, however, a Rattle was given by a female on or near its nest when other Steller's or scrub jays were close to the nest. Also, loud outbursts of calls in the territories of neighboring jays often elicited Rattles by a female in her own territory. And Rattles were also sometimes given at people in situations in which there were no other jays around to elicit the call. On one occasion a Rattle was given by a female on her nest only 2 feet away from the observer. A female was once observed Rattling before and after attacking a mounted screech owl (*Otus asio*), but this was the only time that the call was observed to be used in mobbing.

Courtship.—The contexts discussed above in which Rattles were observed could all be described as agonistic. The fact that females commonly gave Rattles in close temporal proximity to courtship or while being courted raises the question of whether its use in such cases was an aggressive response to the male, or had a function specifically connected with courtship, or both.

In the nonbreeding season, females were observed Rattling as an aggressive response toward their own mates. Supplanting of the female by her mate was common in the nonbreeding season, but it disappeared in the period of nest building and was absent throughout incubation and brooding; the absence of this type of supplanting probably ended with the inception of the fall molt or with the independence of the young. Usually a female submitted to the supplanting attack of her mate without offering any resistance. However, Rattles were observed in one female on two occasions in the winter when her mate landed abruptly a few inches from her on a table and once subsequently supplanted her. Therefore, it appeared that the Rattle could be given as an aggressive reaction by a female to her own mate when he approached too closely.

In the early days of courtship the female commonly Rattled continually when the mate was displaying and approaching her, perhaps in response to his unusually close approach. In the later days of courtship and also during incubation, courtship and mounting generally occurred without the Rattle. That the Rattle was given by females in situations in which only the mate was present,

indicated that jays other than the mate need not have been responsible for eliciting it. Since mounting did not seem to occur in those periods of courtship when Rattles were most common, the Rattle in such situations may have been a reaction of the female to the close approach of the male which subsided as she became accustomed to his persistent approaches in subsequent days.

At the time when courtship was most common, the male constantly accompanied the female, leaving her usually only to chase away other jays from the nest area. Courtship seemed to be stimulated when two or more pairs met at a territorial boundary or other neutral area. After periods of more aggressive calling and displaying, the members of each pair began courting. There was much calling, including Rattles, at these times, and groups of 4 to 8 or more jays were commonly seen. These were usually pairs that were resident in the area, but a few unpaired birds sometimes watched.

When two or more pairs were together at their territorial boundary, the presence of a rival pair seemed to be an important factor in eliciting Rattles. Under these conditions it could sometimes be seen that a female would Rattle in response to any sudden change of position of a rival male or female. Periods of aggressive calling between pairs tended to alternate with quieter periods when courtship occurred. For a few days during the preincubation phase a pair sometimes gave the appearance of actively seeking such social stimulation by touring the neighboring territories and evoking Rattles and other calls wherever the couple went. On such days Rattles from the groups of courting jays were very conspicuous. It may be that the Rattle, as a call apparently unique to females, serves in this species to attract both mated and unmated jays to centers of courtship activity, thus facilitating courtship in mated jays and pair formation in unmated ones. So it seems possible that although the Rattle appeared to be given as an aggressive response even in courting groups of jays, it may still serve an important function in pair formation. In already mated jays it may have been indicative of the rise in the female's aggressiveness coincident with the male's loss of dominance over her, and also it may have reflected the female's initial reactions to the persistent close approaches of the male during courtship.

INTEGRATION WITH OTHER BEHAVIOR

The occurrence of Rattles has been shown to be correlated with a moderately low crest angle and an absence of tail-flicking and Wing-flicking (tables 14 and 15; fig. 8). This relationship suggests that Rattles were characteristically associated with a comparatively low level of agonistic arousal (see the section entitled *Integration of Agonistic Behavior*, below). The frequent use of Rattles in simple supplanting attacks in which no resistance was encountered is also consistent with this hypothesis.

The use of Rattles in supplantings and in the context of a threat against other jays suggests that the NBM's for attack were more active during Rattles than during other calls made with the crest at similar angles, such as Gutturals or *Ow*'s, and that the NBM's for escape were less active than the NBM's for attack.

BEHAVIOR ELICITED BY RATTLES

Sometimes it was possible to observe a change in the behavior of certain jays immediately after they heard a Rattle. When a female arrived at a table and Rattled, some jays would leave immediately after the Rattle and some would remain. In other contexts too, opponents would sometimes leave just after hearing a Rattle. Sometimes the bird hearing a Rattle in an adjoining territory would answer with another Rattle. A Rattle by an intruder in a territory generally had the effect of attracting the female territory owner, who then would make some sort of aggressive response until the intruder left. Thus it appears that the reaction of jays hearing a Rattle generally seemed to follow the pattern set by the preëxisting dominance relationship between the caller and the hearers. On hearing a Rattle a dominant jay generally paid no attention unless the call came from within its territory; but subordinates would sometimes show avoidance of the caller.

MUSICAL NOTE

The Musical note, or Musical, was a common call of males, and was never heard from a female (see also table 2). Both mated and unmated birds gave the call, although it was usually given by mated males with territories.

FORM AND INDIVIDUAL VARIATION

The Musical note lacked the loud, harsh, noisy qualities characteristic of the more common and conspicuous calls for the Steller's jay. It resembled a high, muted whistle given usually all on one pitch and ending abruptly with a slight popping sound audible only at extremely close range. The notes could last almost half a second each and they could be repeated slowly or rapidly from one to several times.

Individual variation in the Musical was easily detectable. Individual (banded) males in the study area could be fairly consistently recognized by the different ways in which they gave the call. For example, the call of X-YY could be represented as a high "*toodle-oot*," the call of O-RXR as a high "*oot*," and that of XY-OO as a low "*woot*." Differences in frequency of use of these variants are shown in table 13. All these variations had the same tonal quality and the same abrupt ending; they differed primarily in pitch and syllabification.

POSTURE

No special posture accompanied the Musical. It was given from a variety of positions on a perch or in flight. When the jay was perched, the head and neck were sometimes slightly extended. The tail and wings were not usually flicked, nor was the tail spread (table 14). In a sample of 38 observations the tail was flicked twice and spread twice, and the wings were flicked once.

The angle of the crest was observed to range from 0 degrees to 80 degrees, but in 59 per cent of 137 observations involving 18 banded and a few unbanded jays it was 30 degrees or lower, the most frequently observed angles being 20 degrees and 30 degrees (fig. 8). In some cases, higher angles were correlated with the bird's having alighted recently, or with resistance by the opponent.

CONTEXTS

Seasonal frequency.—The seasonal frequency of Musicals heard in the study area is indicated in figure 1. The Musical was recorded in every month, but was most frequent in the preincubation period in March and April, and again on warmer days in the autumn. It was least common in the winter, from November through February.

TABLE 16
DIFFERENTIAL USE OF VARIOUS CALLS BY INDIVIDUAL MALE STELLER'S JAYS

Banded caller	Number of encounters							Total number of encounters
	Musical	Shook	Guttural	Wah	Growl	Too-leet	Tee-ar	
O-RXR.....	30	20	23	1	10	15	..	99
X-YY.....	30	16	24	16	3	3	..	92
XY-OO.....	42	16	4	3	65
YRY-X.....	8	16	8	10	9	3	..	54
OOO-XRO... ..	3	28	1	..	3	1	..	36
VR-RR.....	12	13	2	2	29
RV-VRX.	2	12	2	2	6	24
All others.....	16	4	4	1	2	4	2	33
Total encounters....	143	125	68	35	33	26	2	432
Per cent.....	33	29	16	8	8	6	+	—
At males.....	130	113	53	24	29	22	2	373
At females.....	6	10	5	10	1	1	..	33

NOTE: The separate encounters between banded jays are classified according to the types of call given. These data are for encounters between individuals only, and do not include encounters in groups or between pairs. The data were collected in the period March, 1959–April, 1960, inclusive. Similar data for females are in table 17. The contexts of calls in the period January–April, 1960, inclusive, are listed in table 20. Guttural notes, being less easy to hear at a distance, were probably more common than indicated; therefore, the data for Gutturals, unlike the data for other calls, must be regarded as minima.

Agonistic situations.—In table 19 are recorded the social contexts at times when the crest angles were being recorded. These data should not be interpreted as an accurate estimate of the frequency of use of the Musical in each social context, since they were not gathered systematically for that purpose. But the fact that 96 per cent of the 52 examples of this call for which data on the social context were available were of birds in a threat situation, indicates that the call was usually associated with aggressive behavior. Since generally only the supplanting bird in an encounter would give the call, the Musical was closely integrated with the NBM's for attack.

In table 20 are presented the numbers of encounters in which each call except the Guttural was employed in different types of aggressive encounters between individual banded jays. The observations were taken whenever a single banded jay could be recognized as eliciting a call in another jay. Therefore, they represent encounters between single individuals, and do not include calls used in larger groups or between species. These data, which were recorded independently of those in table 19, agree in indicating the Musical as the most commonly used

call by males in supplanting contexts, with the unlikely but possible exception of the Gutturals.

Although the data for Aggressive Sidling in tables 20 and 19 are meager, reviewed in conjunction with the data in table 21 they indicate that the Musical was employed much less often than the *Shook* in this activity. The latter call was generally accompanied by a higher level of agonistic arousal than was supplanting. Similarly, in jays that were chasing other jays out of their territories, the Musical was rarely observed (table 21, Aerial chasing), nor was it ever recorded in jays that were mobbing a predator.

Table 16 shows that of a total of 136 Musicals given at jays of known sex in individual encounters, 130 were at males and only 6 at females.

When the locations where Musicals were given were plotted on a map it was found that virtually all were given within or near the border of the territory of the caller, as was generally true of the other calls. Calls were sometimes given by jays who appeared not to have territories or mates, or who were relatively far from their territories, but these occurrences were unusual.

Individual differences in frequency of use of calls.—The differential use of various calls in aggressive encounters between individuals by color-banded male Steller's jays is shown in table 16. The 3 individuals for whom the greatest number of observations are available used the Musical more often than any other call in this context. In 4 other individuals, however, the Musical was not the most common call, and it ranged from a close second (VR-RR) to relatively rare (OOO-XRO, RV-VRX). The predominance of the *Shook* instead of the Musical in OOO-XRO and RV-VRX is correlated with their subordinate positions, although this cannot be said of YRY-X, who was very aggressive. Both OOO-XRO and RV-VRX held relatively small breeding territories, were low in dominance hierarchies outside of their own territories, and sometimes were not dominant even in areas which had belonged to their own breeding territories. Having a subordinate position, these individuals may have been less confident in aggressive encounters and consequently reached higher levels of agonistic arousal, which were correlated with *Shook*'s, more frequently than was necessary for their more confident neighbors.

Individual variation in use of calls in a different set of aggressive contexts is shown in table 18, in which the initial call given by the dominant jay on arrival at a picnic table bearing a group of jays was recorded. For XY-OO the proportion of Musicals given was similarly high in both situations; but for X-YY and O-RXR, Musicals were much less frequent in group situations than in individual encounters. Out of 51 occasions the Musical was given 27 times by XY-OO, but it was given on only 8 occasions out of 103 by the other 4 individuals observed. Since the calling jay was just arriving, and since there was often a fair number of rival jays on the table, a higher level of agonistic arousal may have been elicited than in a simple supplanting encounter between two individuals. Such an interpretation is supported by the higher modal crest angles found with the predominant calls, 70 degrees with *Shook* and *Wah* as opposed to 30 degrees with the Musical. No explanation is apparent for the greater use of Musicals by XY-OO, but such uncontrolled factors as a possibly lower average number of opponents or the greater shelter by surrounding oaks in his territory, might have had some influence.

Situations eliciting Musicals.—As has been noted above, Musicals were observed primarily in intraspecific aggressive contexts, especially in threats or supplanting attacks at individual males trespassing within the caller's territory. The most frequent situation eliciting Musicals occurred when bait was used to attract jays from other territories into the territory of the caller. The caller then used the Musical in supplanting, but generally did not chase the trespassers any farther than was necessary for him to obtain free access to the bait. The call was also used when intruding jays were near the caller's nest, in which case they were supplanted or chased repeatedly until they left the vicinity. It was occasionally directed at human visitors in the territory, and has been given at the investigator while he was climbing within a few feet of a nest with eggs. It was once observed to be given near the caller's nest at a scrub jay, which was subsequently chased away—one of the rare occasions on which a Steller's jay was seen to dominate a scrub jay.

In groups of courting pairs the Musical was at intervals heard commonly, but it appeared to be used at these times mostly as a threat toward other males rather than as a part of courtship. At some times, however, it did seem to be elicited by the female while the male was Sidling or Circling, especially if she Rattled. In these groups there was a strong correlation between the occurrence of Rattles and Musicals; the two types of calls were commonly heard together, and not generally with other calls. Both were sex-specific and might be suspected to have a special role in pair formation and as behavioral isolating mechanisms.

BEHAVIOR ELICITED BY MUSICALS

When a sudden change in behavior was observed in a jay which had just heard a Musical, it was generally an avoidance of the caller. If given during Aggressive Sidling the same or a different call was often given in response. In one group of courting jays giving Gutturals, the sound of a Musical from the group was followed by abrupt silence. In most of these groups the change in behavior of jays hearing the Musical may have been affected not only by the "releasing value" of the call as such, but also by its effect in drawing attention to and announcing the presence of the dominant jay. Visual signals from the caller probably also affected the opponent.

Reactions of other species to the Musical were not observed, although such reactions were common to the louder, harsh calls.

Ow

The call designated as *Ow* was not recognized as being consistently differentiable from the Guttural until quite late in this study. Consequently, observations of it were not as numerous as desirable, and a number of points about it remain uncertain. *Ow* was considered to be merely a variant of the Guttural until it was realized that it had been observed only in females (table 2). Early in the study there were 3 records of an *Ow* given by 2 males (X-YY, OGO-OX), but since then *Ow* has been observed only in females, never in males. Because the early records of *Ow*'s by males were made before the call was consistently recognized, and because these occurrences were not subsequently duplicated in more than two years of observa-

tions, they may be viewed with some skepticism. The available evidence strongly suggests that *Ow* was primarily, if not exclusively, a female call.

FORM

The *Ow* was similar to the *aap* form of the Guttural, but was higher, more nasal, and louder, ended less abruptly, and resembled the sound "*ow*." Often it was repeated in short series of indefinite length at the rate of about one every second or two.

TABLE 17
DIFFERENTIAL USE OF VARIOUS CALLS BY INDIVIDUAL FEMALE STELLAR'S JAYS

Banded caller	Number of encounters					Total encounters
	Rattle	Shoek	Wah	Guttural	<i>Ow</i>	
XW-WW.....	39	14	3	1	..	57
MO-MXV.....	16	1	..	3	4	24
XRR-RV.....	9	9
XWW-RGW.....	5	2	7
4 other individuals.....	5	3	2	10
Total encounters.....	74	20	5	4	4	107

NOTE: The aggressive encounters between banded jays were classified by the types of call given. These data are for encounters between individuals only and do not include encounters in groups or between pairs. The data were collected in the period March, 1959-April, 1960, inclusive. Similar data for males are in table 16. See table 16 for comment on Guttural.

POSTURE

The *Ow* was given from roughly the same postures as those associated with Guttural notes; it was often associated with various degrees of Wing-spreading. The tail was sometimes flicked, and mild spreading of the tail was sometimes observed. The modal crest angle for 24 observations was 30 degrees, with 22 of the 24 observations in the range of 10-50 degrees (fig. 8).

CONTEXTS

Like the Guttural, the *Ow* was recorded in every month, but was most common in the preincubation period, in March and April.

The call was rarely observed in aggressive encounters between individuals. Table 17 shows that *Ow*'s were recorded in only 4 of 107 such encounters in which vocalizations were used. It was commonly heard in encounters between pairs, such as those which occurred in territory border zones and were frequently associated with courtship activities. The *Ow* was not normally associated with actual attacks, fights, or chases. On a few occasions it was given at the observer when no other jays were near enough to have been the cause.

On March 29, 1959, in a courtship group of seven jays which consisted of three pairs and an onlooker, one female was observed giving the *Ow* call continually. Then she began Rattling continually as the male began to Circle her. When the male stopped Circling, she began the *Ow*'s and ceased Rattling. These calls were again replaced by Rattles when the male resumed Circling. Thus, in this case the

Ow was not given during active courting by the male, but only between those periods. The call was frequently observed in territorial disputes between females where no males were involved, and on those occasions the activation of sexual NBM's should have been absent.

Because the *Ow* normally occurred in birds gathered in groups, was frequently repeated, and was often given by more than one bird, it was difficult to observe any definite reaction to it by other jays. In one observation, a jay calling *Ow*'s was vigorously attacked and chased by a female jay, and in another observation the *Ow* seemed to cause another jay to leave. It seems probable that the call served mainly to attract attention to the mood of the caller, and that considerations of location, dominance, and sexual state played a large part in determining the subsequent reactions of other birds.

GROWL

The Growl was observed to be given by both sexes, although it was given primarily by males, as is indicated in table 2.

FORM

"Growl" is perhaps an inappropriate name for this call, since it only vaguely resembled the growls of other animals, such as dogs or cats. The Growl of the Steller's jay sounded like the *Wah* and might have been interpreted as an extreme variant of it, but was quite consistently differentiable from the *Wah* and was employed in different contexts. The Growl was generally given in phrases of two notes, each conspicuously down-slurred, with the initial higher-pitched part of each note having a suggestion of a musical quality and the lower-pitched terminal part having a harsh rasping or grating quality. The call was usually given loudly, and the sequence of two notes was often repeated several times, though not nearly as rapidly or as often as were *Shook*'s or *Wah*'s.

POSTURE

Growls were observed in a jay in flight on one occasion, but they were usually observed in perched jays. The modal crest angle of jays giving Growls on 39 occasions was 40 degrees, and 64 per cent of the observations were of jays with angles of 40 degrees or less, although the angles ranged from 0 degrees to 90 degrees (fig. 8). Tail-flicking and Wing-flicking were common, and tail-spreading was occasional (table 14). Jays giving Growls have been seen to thrust their heads forward with the bill inclined upward as much as 20 degrees; with each call, sometimes, the tail was spread slightly, and concurrently the tail and wings were flicked upward. The call was also given in the posture of Aggressive Sidling.

CONTEXTS

Growls were recorded in every month of the year, with a peak in March and April. They were least frequent in October and November. There was a slight increase in frequency in August.

The Growl was not a common call in any easily categorized behavioral context. Of 108 calls recorded during Aggressive Sidling, only 3 were Growls (table 21).

During aggressive encounters of various kinds between individuals not in groups, Growls were recorded in none of the 107 encounters in which females called (table 17), but were noted in 33 of the 432 in which males called (table 16). On 154 occasions when dominant males arrived at a table occupied by subordinate jays, the initial call was a Growl only once (table 18). Growls were also rare in jays which were fighting, chasing, or mobbing (table 21); or in the hand, flying from the hand, or alighting after release (table 22). That Growls, when they were used, were employed by jays with a strong activation of NBM's for aggression, is suggested by the observer's impressions in the field and by the data in tables 19 and

TABLE 18

INITIAL CALLS GIVEN BY DOMINANT MALES IN THEIR OWN TERRITORIES WHEN ARRIVING AT PICNIC TABLES OCCUPIED BY ONE OR USUALLY MORE JAYS OTHER THAN THEIR MATES

Banded caller	Number of encounters						
	<i>Shook</i>	Musical	<i>Wah</i>	Guttural	<i>Too-leet</i>	Growl	N
XY-OO.....	9	27	5	10	51
X-YY.....	15	2	9	6	2	..	34
YRY-X.....	12	1	11	4	..	1	29
VR-RR.....	12	2	9	23
O-RXR.....	5	3	1	4	4	..	17
Total.....	53	35	35	24	6	1	154

NOTE: The data were recorded in February and March, 1959. Notice the more frequent use of the Musical note by XY-OO than by other individuals.

20. These data show that almost all of the observations were of jays engaged either in supplanting, in Aggressive Sidling, or in calling at another jay without supplanting it. Occasionally Growls were given at the observer, and once at a scrub jay that was beneath the nest of a Steller's jay.

BEHAVIOR ELICITED BY GROWLS

Since Growls were usually employed at close range, it was difficult to distinguish reactions to the calls from reactions to the visual stimuli, and no observations were made on situations in which these two aspects could be separated. This in itself contrasts with my general observations on some of the other calls, such as *Shook* or *Wah*, in which the hearing of the call from jays definitely out of sight often elicited a behavioral reaction. On one occasion when a male landed on a garbage can just outside of his territory, a Growl given by the dominant male 20 feet away was followed by an immediate retreat by the intruder back into his own territory.

WAH

The *Wah* was one of the two calls of the Steller's jay which were heard commonly in all months and which are familiar to the casual observer of birds, the other call being the *Shook*. Anyone who is at all familiar with Steller's jays has almost certainly heard these calls many times. As reflected in table 2, the *Wah* was given by both sexes, 36 per cent of a series of 194 observations of jays of known sex

being records of females. This was the second highest percentage by females for any call which was used by both sexes.

FORM

The *Wah* had a noisy quality such that an individual call could not be easily assigned to particular notes on a musical scale, as could the calls with a whistled or musical quality, such as the Musical, the *Tee-ar*, and the *Too-leet*. The sound of "*wah*," if pronounced with a harsh and nasal quality, indicates to some degree the

TABLE 19

CONTEXTS IN WHICH STELLER'S JAYS WERE OBSERVED GIVING VARIOUS CALLS

Context	Number of observations						Total
	Rattle	Musical	Growl	Wah	Too-leet	Shook	
By supplanter.....	25	29	4	8	5	16	87
By supplanter.....	2	2
At individual but no supplanting	12	19	5	5	1	22	64
Aggressive Sidling.....	..	2	6	2	7	32	49
In fight.....	1	..	2	3
After fight.....	1	1	2
Mobbing.....	1	31	32
Just alighted.....	26	..	2	28
On picnic table.....	28	28
Appeasement.....	1	1
Answering at a distance.....	2	2
Courtship.....	8	2	10
Total.....	49	52	15	103	13	76	308
Context unspecified.....	78	88	2	131	17	77	393

NOTE: These data are limited to observations made at the time of recording of crest angle. Not all calls are listed. The contexts which were recorded were primarily those which could be described in a few words; consequently, many were unspecified at the time of observation.

lack of an abrupt beginning and end to the call and something of its tonal quality. There tended to be a slight downward inflection at the end of the call. The *Wah* was given singly or in a rather slow series of indefinite length, usually little faster than one per second and generally much slower than a series of *Shook's*.

POSTURE

The postures of jays giving the *Wah* were characteristic of the activities in which they were participating, rather than of the call itself. One of the most frequent of these activities was mobbing, but the call was also given in submissive begging, by juveniles begging for food, and in Aggressive Sidling.

In mobbing an owl, the jay approached to within a few feet and sometimes dove at the owl from above and behind. Usually the crest was quite high, the legs were flexed, and the body was lowered toward horizontal, ready for a quick take-off. The ducking, bowing, or bobbing movements of body and tail together so characteristic of the scrub jay in similar circumstances, were uncommon in the Steller's jay. However, the tail was often jerked up rapidly with each *Wah* and allowed to

lower gradually between flicks. The tail was frequently slightly spread during these flicks and sometimes spread to a greater extent as the owl was more closely approached. The wings also were sometimes flicked in high-intensity mobbing.

Another frequent posture in which the *Wah* was given was adopted when a jay had just alighted in a spot which was unfamiliar or associated with danger in some way. Then also, the crest was high and the tail flicked. The postures involved in gaping, appeasement begging, and Aggressive Sidling from which the *Wah* was also given, have been discussed above.

TABLE 20

NUMBER OF ENCOUNTERS IN WHICH DIFFERENT CALLS OF MALE STELLER'S JAYS WERE OBSERVED IN VARIOUS TYPES OF AGGRESSIVE ENCOUNTER BETWEEN BANDED INDIVIDUALS

Aggressive context	Number of encounters in which call was used					
	Musical	Shook	Wah	Growl	Too-leet	Total
Aggressive Sidling.....	1	10	2	13
By supplanting jay:						
Before or during.....	22	15	2	3	..	42
After.....	9	3	4	2	..	18
By supplanted jay.....
Threat, but no supplanting or sidling....	5	1	1	1	..	8
Total.....	37	29	7	6	2	81

NOTE: All vocalizations except the Guttural notes were recorded. Data were collected in the period January-April, 1960, inclusive. They are for encounters between individuals, and do not include encounters in groups or between pairs.

The crest was at any angle from 0 degrees to 90 degrees during delivery of the *Wah*, but in 68 per cent of the 233 observations the angle was 60 degrees or greater, the mode lying at 70 degrees (fig. 8). The tail was usually flicked and was sometimes spread during the *Wah*, and the wings were sometimes flicked slightly off the back, as shown in table 14. The high frequency of tail-flicking was correlated with the frequent use of the *Wah* just after alighting and in mobbing. Wing-flicking was most often detected during intense mobbing.

CONTEXTS

Seasonal frequency.—Although the *Wah* was heard commonly in every month, it was observed, along with other vocalizations, to increase in frequency in March and April. There was a decline in frequency correlated with the increased number of incubating females in April and May, and a further decline occurred in the cooler months of November and December.

Agonistic situations.—The principle use of the *Wah* was in agonistic situations. This is reflected in table 19, which shows that most of the observations for which crest angles were recorded during *Wah*'s were of jays that were either mobbing or at or near a picnic table. Since jays were often attracted from other territories to these tables, supplantings often occurred there. Also, the association with man

and the lack of cover may have contributed toward the appearance of nervousness displayed frequently by jays on picnic tables, especially those which were newly arrived. The *Wah* was not observed to have any role in courtship, although it did sometimes occur among groups of courting birds as an aggressive response between pairs.

Uncommonness in individual encounters.—The *Wah* was used primarily in agonistic contexts, but its use in such situations differed significantly from that of other calls. In encounters between known individuals the *Wah* was used infre-

TABLE 21
DIFFERENTIAL USE OF CALLS IN CERTAIN AGGRESSIVE CONTEXTS

Call	Aggressive Sidling	Aerial fighting	Aerial chasing	Group mobbing perched owl	At perched or flying accipiter
<i>Shook</i>	56	7	25	..	5
Musical..	26	..	4
<i>Too-leet</i>	8	..	1
Guttural.....	8
<i>Wah</i>	3	2	..	12	9
Growl.....	3	..	1
<i>Tee-ar</i>	3
Rattle.....	1	..	2	1	..
<i>Ack</i>	1	..
Total.....	108	9	33	14	14
Male.....	90	1	28
Female.....	5	..	4
Sex undetermined.....	13	8	1

NOTE: The occasions on which different calls were observed are classified according to aggressive context. Calls were not usually given during aerial fighting, but normally accompanied Aggressive Sidling and aerial chasing. Data for males and females were combined in the table; of the five instances when calls were given by females, four were the Rattle and one was the *Shook*. The remainder was given by males.

quently in comparison with other calls. Table 17 shows that females used the *Wah* in only 5 of 107 such encounters, and table 16 shows that males used it in only 35 of 432 such encounters. In 60 of these encounters in which the calling jay was the victor in a supplanting, the *Wah* was used only 6 times (table 20). On 108 occasions when calls were given by jays in Aggressive Sidling, *Wah*'s were given but 3 times; and of 27 calls given by jays while flying after a fleeing opponent none were *Wah*'s.

On alighting.—The relationship between *Wah*'s and tail-flicking shown in table 14 is related to the frequent use of *Wah*'s just after alighting and in mobbing. Dominant jays that gave the call just before or after their arrival at a table occupied by one or more other jays, used the *Wah* on 35 of 154 occasions (table 18). In these instances there were often not one but several jays present, and the caller was not necessarily involved in supplanting. Although the *Wah* was not the most frequent call in that context, its frequency was higher than in encounters strictly between individuals. In 104 instances in which the contexts of *Wah*'s were recorded (incidental to the recording of crest angles), the jay had just landed on a picnic table on 26 occasions; and on 28 additional occasions the jay was also

on the table but was not recorded as having just landed (table 19). Other jays were generally not present at these times.

The frequency of *Wah*'s given on alighting rather than in flight is indicated in table 22, which records the calls given by jays that were held in the hand during banding then released and watched in flight and just after alighting. Of the calls that were given in flight, only a small percentage were *Wah*'s but of the calls given just after alighting, *Wah*'s were by far the most common. Tail-flicking was invariably observed at these times, and frequently Wing-flicking also.

TABLE 22
VOCALIZATIONS GIVEN BY STELLER'S JAYS DURING BANDING AND AFTER RELEASE

Call	In hand	During flight from hand	On landing after release
<i>Shook</i>	2	17	2
<i>Wah</i>	6	4	17
<i>Cack</i> (Squawk).....	1	1	..
Growl.....	1
Guttural.....	1
Records of calls.....	9	22	21
Recorded as silent....	1	83	36
Unspecified (probably silent).....	143	47	97
Total.....	153	152	154

NOTE: All or almost all of the unspecified cases were of silent jays. Only one type of call was given by each individual in a particular context, except for two jays which gave both *Wah* and *Shook*.

Mobbing.—The most conspicuous and commonly observed use of the *Wah* was in mobbing certain predators. In mobbing screech owls or great horned owls (*Otus asio*, *Bubo virginianus*), which were either alive and perched or were mounted, large groups of jays often accumulated. These jays gave only *Wah*'s at the owl, with the exception of a few *ack*'s or Squawks occasionally or a Rattle rarely (table 21). Other calls were frequently heard from such mobbing groups, but these were observed to be given invariably at other jays rather than at the owl. Since the group was often trespassing within an individual jay's territory, disputes between jays were frequently seen in such gatherings. Other situations may have elicited various calls among the mobbing jays, but jays which were seen to be approaching and calling at the owl almost invariably gave *Wah*'s. On one occasion when a great horned owl took flight and flew about 200 feet, the group of jays all ceased giving *Wah*'s and called *Shook*'s as they flew after the owl. This observation was consistent with the observed correlation between *Wah* and perching and between *Shook* and flying or chasing (see table 21).

The most frequently observed hawk in the study area was the Cooper's hawk (*Accipiter cooperii*); the sharp-skinned hawk (*Accipiter striatus*) and the red-tailed hawk (*Buteo jamaicensis*) were also seen occasionally. Of 14 occasions when calls were observed to be elicited by an accipiter, the *Wah* was given on 9, and on the other 5 occasions, the call *Shook* (table 21). There seemed to be a tendency for jays who were diving for cover or who were startled by the sudden perception

of a flying accipiter to give *Shook's*. Jays which were perched in good cover and mobbing a perched accipiter or one flying at a distance usually gave *Wah's*. Generally the behavior toward accipitrine hawks resembled that toward owls, in that *Wah* was the most common call, but the active hunting habits of these hawks led to greater variability in stimulus situations, which in turn resulted in increased variation in the calls elicited.

Other animals occasionally elicited *Wah's*. A cat elicited *Wah's* when inside a trash barrel or under a picnic table, but rarely when walking in the open. When a tame fox walked away from some food, a jay gave *Wah's* before going to the food. *Wah's* were not observed to be given at low-flying turkey vultures (*Cathartes aura*) or red-tailed hawks. A male jay who was being repeatedly dived at by a Western wood pewee (*Contopus sordidulus*) gave several *Wah's* at the pewee after a few dives.

The most frequent call given at the human visitors in the study area was the *Wah*. Jays were recorded giving *Wah's* at people at least 20 times. Many of these cases were in situations in which the person was close to some food to which the jay later went, or situations in which he was in some way frustrating the jay's foraging behavior. Mobbing of human beings by jays rarely occurred unless the intruders were robbing a nest. People were generally either avoided or watched for food, and were not treated as were the owls or accipitrine hawks.

Other situations.—As mentioned earlier, the *Wah* was the usual call accompanying appeasement begging and gaping of adults. The subsection on appeasement begging in the section entitled *Postures and Movements*, above, may be consulted for a discussion of the contexts in which such displays occurred. Full-grown juveniles begging for food from their parents also used the *Wah*. Some juveniles appeared to call at the slightest frustration; one was seen in early August giving *Wah's* just after having failed to catch a fly. It then approached its parent, gaped, and gave further *Wah's*.

INTEGRATION WITH OTHER BEHAVIOR

A relatively high level of agonistic arousal in jays giving the *Wah* was indicated by (1) the loud, vigorous manner in which the call was delivered; (2) the tail-flicking that usually accompanied it; (3) the Wing-flicking that occasionally accompanied it; (4) the high modal crest angle (70 degrees); and (5) its use during the mobbing of relatively large and dangerous species such as owls, accipiters, cats, and people. Mobbing jays were active, alert, and vigorous in their behavior. Jays giving *Wah's* on alighting after release from the hand or on a picnic table were also alert and quickly reactive to slight danger stimuli. *Wah's* were also observed in jays which were not especially aroused, as judged by these criteria, and generally the calls were weaker and fewer, the crests were lower, and the tails flicked less vigorously.

A lack of association between *Wah's* and a dominance of the NBM's for attack was suggested by: (1) the infrequent use of *Wah's* during supplanting encounters between individuals in dominance hierarchies when the outcome was largely predetermined; (2) the frequent use of *Wah's* against predators; and (3) the frequent use of the *Wah* outside the caller's territory (in mobbing).

The impression was gained, therefore, that *Wah's* were typically associated with a high level of agonistic arousal and alertness, but not with a strong probability of confident attack. *Wah's* were observed in jays fighting in mid-air, however; and swooping attacks on owls sometimes occurred during mobbing; so occasional attacks certainly occurred. The use of *Wah's* in juvenile begging, in appeasement begging, and by the jay frustrated by its failure to catch a fly, suggest that activation of attack NBM's need not be strong, and may even be absent during *Wah's*. Obviously, the range of stimulus situations which could elicit *Wah's* was great.

BEHAVIOR ELICITED BY WAH'S

Two general types of reaction to the hearing of *Wah's* were observed, attraction and avoidance. A power of attraction was indicated by the large group of jays which often accumulated during mobbing. When only *Wah's* were heard and no mobbing jays or predators were visible, jays could still be seen flying toward the scene of a mobbing. Jays have been observed to cease foraging or other activities upon hearing a series of *Wah's* and fly toward the sound. When a mounted owl was exhibited, the jays sometimes went a long time without noticing it even when it was within view; but as soon as the first *Wah's* had been uttered, it was usually only a short time before a group of jays had gathered around the owl. Jays readily crossed one or more territories to arrive at a group of mobbing jays; so the power of attraction must have been considerable.

The attractive power of the *Wah* was also revealed when sunflower seeds were placed on a picnic table for bait. The first jay to arrive at the bait was usually a member of the pair within whose territory the table stood. Usually on its first arrival this jay would give one or more *Wah's*, irrespective of whether the observer was near the table or was practically out of sight. The calls were fewer and given more slowly than in mobbing. After these *Wah's* jays could be seen flying through the treetops from distant territories toward the baited table. Although the bait may have gone undiscovered for a long period, the *Wah's* of the first-arriving jay usually indicated that a fair number of jays would be utilizing the seeds thenceforth. The occasional times when other types of call were used in similar contexts did not seem to be followed by a gathering of jays.

The avoidance reaction was not as easily observed as that of attraction. Occasionally in jays which used *Wah's* before supplanting attacks it was possible that the call contributed to the quicker escape of the subordinate, although this is debatable. On one occasion a pair was giving *Wah's* at an unbanded jay intruding on its territory; supplanting attacks were not observed, although the pair moved closer to the intruder. The unbanded jay then flew into the neighboring territory and the pair immediately ceased calling. However, this neighboring pair then commenced giving *Wah's* and approaching the intruder, which then left the area. All calling then ended. During mobbing the combined effect of many *Wah's* might also stimulate avoidance in the predator, as it certainly does in some human hunters. Clearly, in these cases the effect of the call by itself could be separated from effects of the other actions of the callers, and an avoidance response to the *Wah's* would not be inconsistent with the field observations.

Other reactions to *Wah's* were sometimes noticeable. In a male who was taking

seeds on a picnic table outside his territory, the sound of several *Wah*'s nearby caused increased watchfulness and a sudden rise in the crest from 20 degrees to 60 degrees. *Wah*'s heard from a few hundred feet or farther away often caused birds to answer back with more *Wah*'s so that jays in several separate areas would take up the call.

TOO-LEET

The *Too-leet* was not frequently heard in the Indian Camp population. On none of the 26 occasions when the crest angle of a jay of known sex was observed was the individual a female (table 2), nor were females ever observed giving the call at other times.

FORM

In common with the *Tee-ar* (see below), the *Too-leet* call had a shrill, whistled quality that set it apart from the more usual calls, which had a rasping unmusical quality. The call was rather high-pitched and consisted of essentially two syllables sounding like "*too-leet*" with the second syllable a harmonic fourth to an octave higher in pitch and receiving the accent. A third and lower-pitched syllable was sometimes added, to make "*too-leet-o*." The call was usually repeated two to four times, sometimes more. In a total of 34 occasions, the call received two repetitions 8 times; three, 13 times; four, 6 times; and five or more, 7 times. This was probably the most variable call in the vocabulary of the Steller's jay from population to population, and it should not be expected that the syllabification described here will fit the calls of any other population than the one in Tilden Park.

POSTURE

Too-leet's were given when a jay was in flight and also when perched. The caller could be in the position of Aggressive Sidling, or it could merely have the head and neck slightly extended. The crest was seen at all angles, but was observed at 70 and 80 degrees slightly more often than at other angles (fig. 8). The wings and tail might be flicked, and the tail spread, although these actions did not typically accompany the call (table 14).

CONTEXTS

Seasonal frequency.—Actual counts of the number of times a series of *Too-leet*'s was heard in the study area (table 12) revealed that the number heard per average composite ten-hour period was highest in the preincubation months of March and April, 1959. A decline in the months of incubation and molt reached its lowest point in July and August. After a brief increase in the warm month of September, the frequency of calls was generally low during the winter.

A significant increase in the frequency of *Too-leet*'s occurred from February through April, 1960, but the frequency did not approach the high frequencies in the same months in 1959. A similar pattern was evident in the percentage of days in the area on which *Too-leet*'s were heard. Days with no calls were most frequent from October through January.

A similar difference between 1959 and 1960 is also detectable in the corresponding data for *Tee-ar*'s in the same table. The lower frequency of calls in March and

April of 1960 than in the same months in 1959 was correlated with: (1) a slight reduction in the number of breeding pairs in 1960, from nine to eight, (2) the disappearance of an aggressive male (X-YY) and his replacement by a less aggressive one (RV-VRX), and (3) the virtual absence of nonbreeding jays in 1960.

Agonistic situations.—Jays observed giving *Too-leet's* while their crest angles were being recorded were mostly engaged in Aggressive Sidling or supplanting (table 19). Courtship, mobbing, and landing on a picnic table were not represented in this sample, nor were *Too-leet's* heard at any time from jays while courting or mobbing. In aggressive encounters between individuals, the call was not observed to be given at all by females (table 17), but was recorded on 26 of 432 occasions when males called (table 16). Of 108 records of calls given during Aggressive Sidling, 8 were of *Too-leet's* (table 21). Of 33 records of calls given during aerial chasing of a rival, 1 was of *Too-leet* (table 21). And of 154 observations of calls given by dominant jays arriving at a picnic table occupied by other jays, only 6 were of *Too-leet's*. Therefore, *Too-leet* was not a predominant call in any of the more common or easily categorized behavioral contexts. However, when it did occur, it was usually in Aggressive Sidling or supplanting.

Individual variation in the frequency of use of Too-leet's.—When the records of vocalizations for all the jays in the Indian Camp area were considered, the proportion of *Too-leet's* was very small. But conspicuous variation was found between individuals in frequency of use of this call; *Too-leet's* were never heard from some individuals, although they were fairly commonly heard from others. Thus, the data for the group as a whole were not typical for many individuals.

In figure 10 the number of records of *Too-leet's* for each of the male territory holders in the study area is plotted on a map showing in dashed lines the approximate locations of territories in the spring of 1959. These data were not gathered in a regular fashion; rather, they were recorded for various other purposes and then combined; consequently, they are only roughly comparable. Special attention was given to those individuals which were not known to give the call or to do so only rarely, but no attempt was made during the course of the field work to keep track of the number of occasions on which *Too-leet's* were given by each individual if they were frequently given by that individual. If this had been done, the numbers for males O-RXR, RY-RYX, and possibly OOO-XRO and the unbanded would have been much higher.

The map (fig. 10) shows that those individuals which regularly employed *Too-leet's* (O-RXR, YRY-X, RY-RYX) plus those which used it rarely (X-YY, OOO-XRO, RXR-OR, and the unbanded) had their territories together in the southern part of the study area. In the northern part of the study area were the territories of the individuals which were never observed to give *Too-leet's* (XMY-YMY, VR-RR, RV-VRX, VO-MVX). Although much time was spent observing X-YY and XY-OO, *Too-leet's* from them were almost never recorded, and the numbers on the map can safely be said to represent the only times that the call was ever heard from them with certainty.

A variety of factors may have contributed to this difference in frequency of use of *Too-leet's* between different males. Steller's jays often answered the call of an

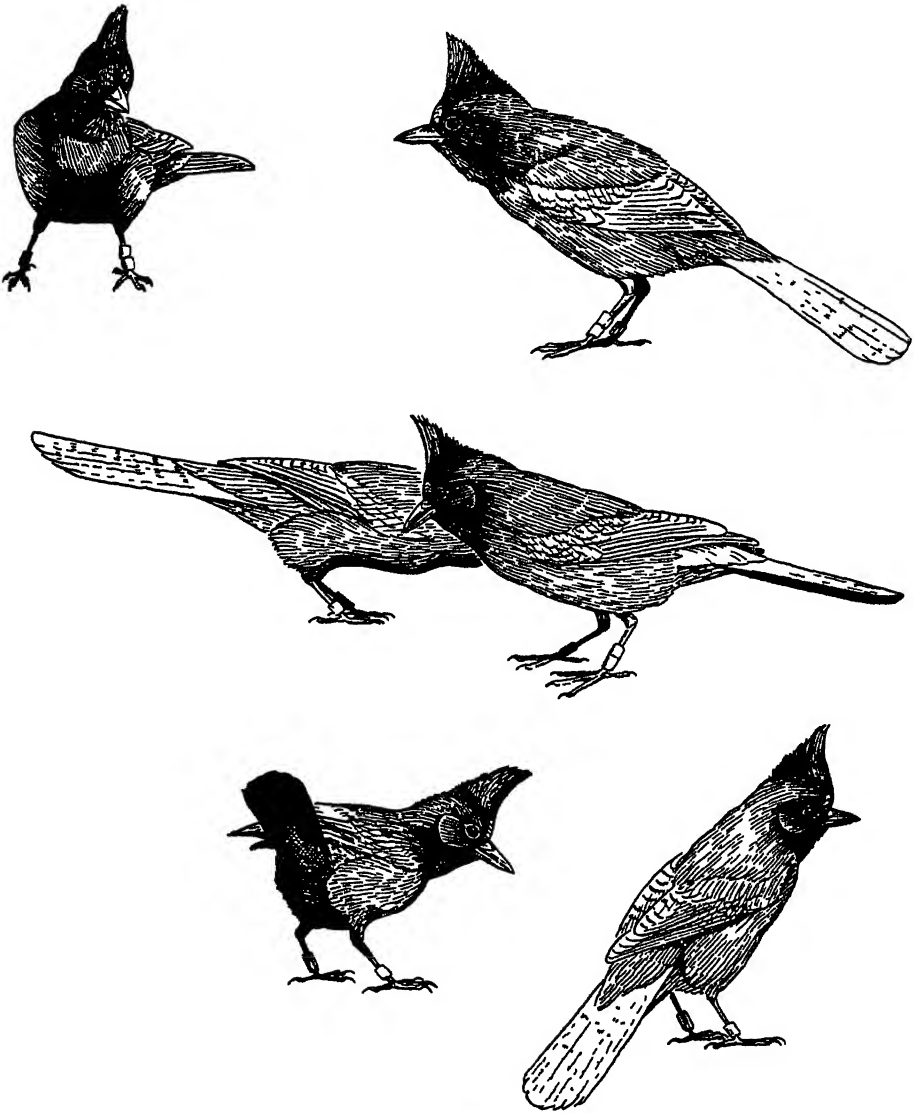


Fig. 9. Three sets of positions taken during Aggressive Sidling in the course of one encounter between two male Steller's jays. Note the erect crests, the predominantly parallel orientation, and the turning of bill and tail toward the opponent. Loud and repeated calling typically occurred throughout such encounters, together with frequent displacement digging or bill-rapping.

opponent using the same call. Thus, if one jay in the area gave a particular call, the other jays would often use it in answering him. Hence, the frequent use of the call by O-RXR may have led some of his closer neighbors to use it also, and vice versa. The predisposition to answer with the same call may also have favored learning of the call at an earlier age, perhaps when the juvenile first arrived in the area and developed a habit of restricting its activities to one particular area. Whether or not the learning of the particular phrasing in this call was any easier

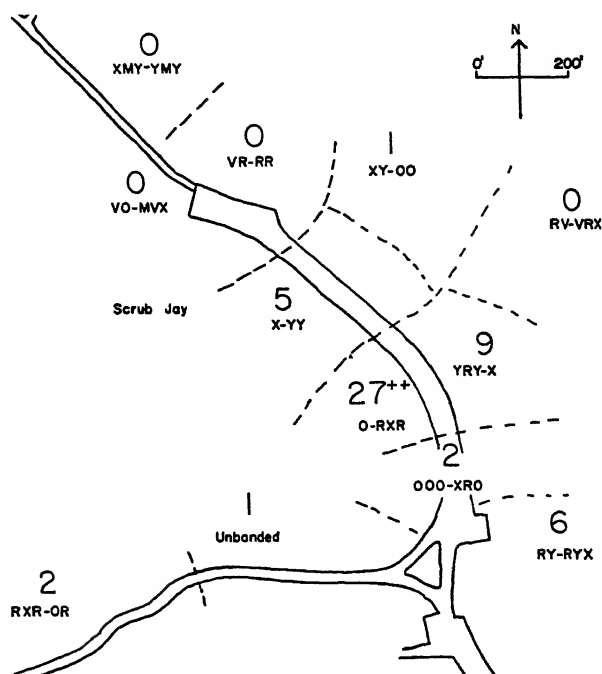


Fig. 10. Variation between individual male Steller's jays in frequency of use of *Too-leet's* in relation to location of territories in the Indian Camp study area. The number of records for each male is plotted within the appropriate territory. Dashed lines indicate approximate territorial boundaries. See table 16 for comparisons of frequency of use of *Too-leet's* with other calls in these individuals.

for the young of parents who gave the call commonly than for the young of parents which did not, for genetic or circumstantial reasons, is an open question.

INTEGRATION WITH OTHER BEHAVIOR

The relatively high crest angles of jays giving *Too-leet's* suggest that the jays usually had a high level of agonistic arousal, although the level could vary widely. The high proportion of *Too-leet's* which was given during Aggressive Sidling further argues for a frequently high level of agonistic arousal. The fact that *Too-leet's* were given during supplanting or Aggressive Sidling suggests that at times the call was given when the NBM's for attack were dominant or at least not subordinate.

BEHAVIOR ELICITED BY TOO-LEET'S

The few observations of changes in behavior subsequent to hearing *Too-leet's* suggest that in its alerting and threatening role the call resembled the *Shook*. In a pair engaged in Sexual Circling and Sidling, the sound of *Too-leet's* from elsewhere was followed by a temporary cessation of courtship. On another occasion a male jay was silently following a man and some small boys as they walked through the picnic area and well into the neighboring territory, perhaps hoping for some

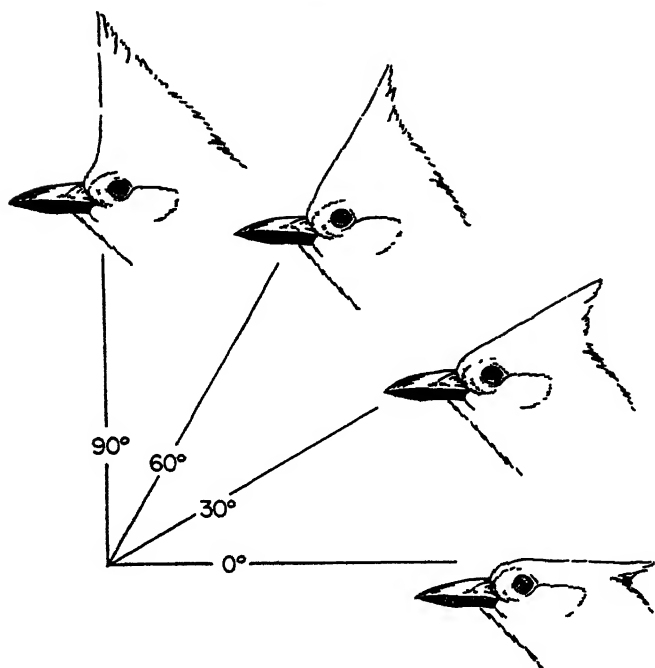


Fig. 11. Range of variation in crest elevation in the Steller's jay, with method for estimating angle of crest elevation.

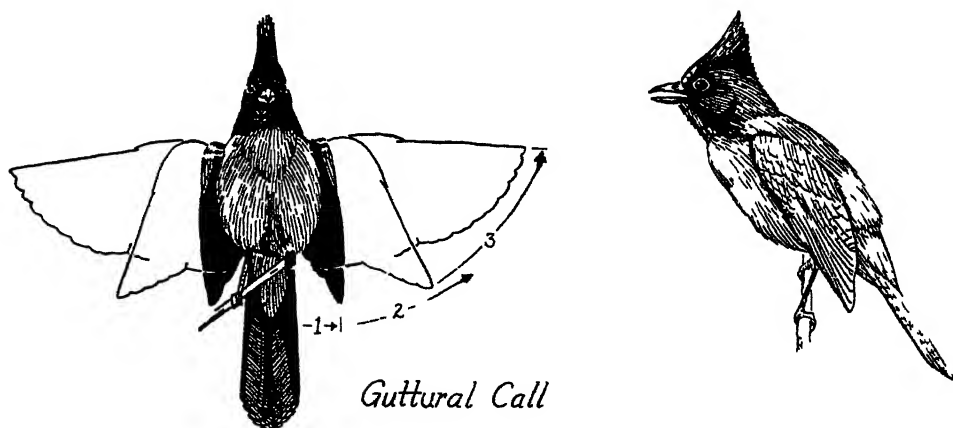


Fig. 12. Wing-spreading with the Guttural call, in front and lateral views. The intensity levels referred to in the text and tables are indicated as 1, 2, and 3.

food. Then the sound of a series of *Too-leet*'s was immediately followed by a silent return to his own territory by the pursuing jay, although he was not being chased and the caller was apparently not in sight. The use of *Too-leet*'s during Aggressive Sidling and supplanting made it difficult to separate the effect of the call from the effects of other stimuli which influenced the opponent's behavior, but presumably the call contributed to the total effect of intimidation.

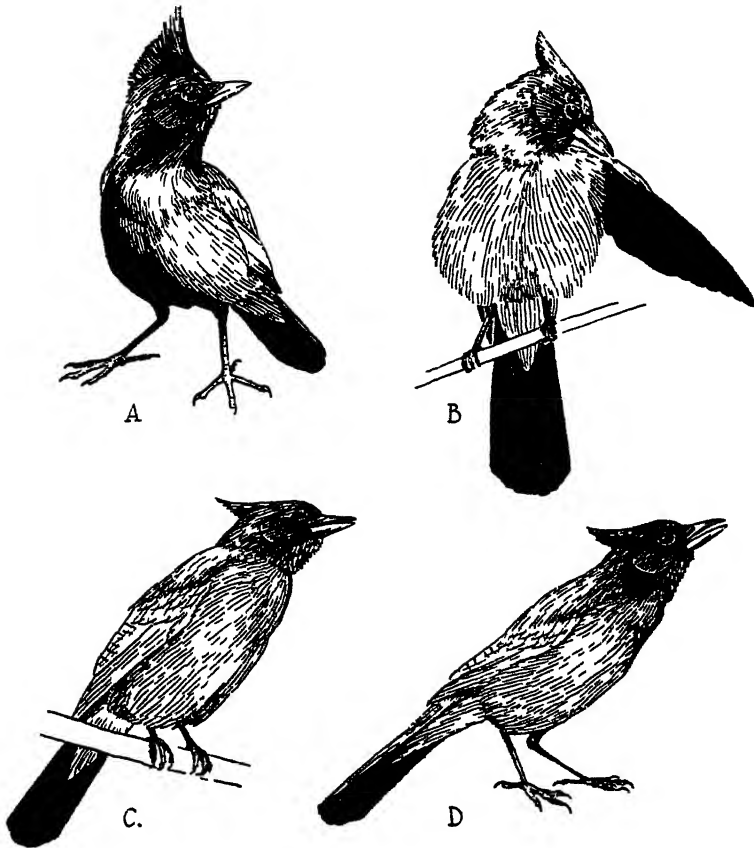


Fig. 13. A, Steller's jay with maximally erect crest, just after alighting at a baited picnic table. B, preening, with crest typically low. C, typical posture during Song. D, position during the Musical call on picnic table before supplanting.

SHOOK

The *Shook* was probably the most frequently heard loud call of the Steller's jay at times other than in mobbing. It was the call most likely to be confused with one of the calls of the scrub jay, at times being difficult to distinguish from the latter if heard at a distance. The *Shook* was given commonly by both sexes in all months, with 12 per cent of a series of 139 observations on jays of known sex being of females (table 2).

FORM

The call resembles the sound "*shook*." It was usually repeated loudly, sometimes as fast as five per second. No other call was repeated nearly as rapidly. On two occasions when the male and female of a pair were calling together, the call of the male sounded more like "*shook*," and that of the female like "*shick*." Thus, there was a suggestion of a slight average difference in the quality of the call between males and females, the females having a slightly higher-pitched, thinner, and more

metallic-sounding call than the males. *Shook's* given by fall juveniles were usually not as loud, and were more variable in quality, and uneven in tone and loudness.

POSTURE

When the *Shook* was given, the jay was in flapping flight, or gliding with spread tail and wings, or perched. When the bird perched, the head was sometimes extended forward and upward slightly, with the bill a little above horizontal and the throat feathers moving perceptibly. The call was often given in Aggressive Sidling.

The crest was usually erect during the *Shook*, although it varied from 0 degrees to 90 degrees. The frequency distribution of 157 observations of crest angles has a mode at 70 degrees, with 63 per cent of the observations at 60 degrees or higher (fig. 8). Tail-flicking was recorded 8 times in 29 observations, tail-spreading 7 times in 30 observations, and Wing-flicking or Wing-spreading no times in 36 observations (table 14).

CONTEXTS

Seasonal frequency.—Heard in every month, the *Shook* was most common during the period of courtship, when jays commonly gathered in groups at territorial borders or within territories. This period was in March and April. The frequency of *Shook's* on a population basis then declined during nesting, rose in the fall when more jays were present, and declined again during the winter (fig. 1).

Agonistic situations.—Like that of the *Wah*, the principal use of the *Shook* was in agonistic activities. Table 19 shows that *Shook's* were given in most cases in an aggressive context. These situations were the following: during or after the supplanting of another jay, while calling at another jay without supplanting taking place, or during Aggressive Sidling. *Shook's* were not recorded as a part of courtship or during mobbing of perched hawks and owls.

In individual aggressive encounters between banded jays, the *Shook* was the second most commonly used call in males (table 16) and females (table 17); these data do not include encounters in groups larger than two or three jays. When some of these data are broken down according to types of aggressive contexts, as in table 20, they suggest that the *Shook* in supplanting was second to the Musical note in frequency of use, and that in Aggressive Sidling it was first. Additional data on Aggressive Sidling in table 21 indicate more conclusively that *Shook* was the predominant call in that context.

When a group of generally three or more jays on a baited picnic table elicited a call from the arriving dominant jay, *Shook's* were given more frequently than any other call by most individuals (table 18).

Shook's were heard from flying jays probably more than any other call. This is indicated in three ways. Table 22 shows that *Shook's* were given on 17 of 22 occasions when calls were given in flight just after a bird had been released from banding. Similarly, *Shook's* were given on 5 of 33 occasions when calls were given in flight by one jay chasing another aggressively (table 21). And *Shook's* were given on 7 of the 9 occasions when calls were recorded during aerial fighting (usually by both birds; table 21). It is interesting to note that *Shook's* were the predominant calls both in escape from the bander's hand and in aerial attack on

another jay. These facts suggest that the criterion of occurrence of acts temporally associated with attack or escape is sometimes open to question as a reliable means of assessing a predominance of the attack or escape NBM's (Criterion 2B in table 25).

Shook's were commonly observed given by jays which were flying or about to fly, when the context was less easily specified. They were usually heard when a group of mobbing or courting jays was dispersing and the individuals or pairs were flying from the scene or about to fly.

Shook's were uncommon in the contexts in which *Wah's* were common, namely in mobbing of perched hawks and owls, and on alighting at picnic tables or in other situations characterized by a high degree of alertness and reactivity to slight danger stimuli. They were, however, sometimes given at hunting accipiters while the jays were diving for cover, in keeping with the correlation of the *Shook* with flying.

Shook's were also given in response to other sudden danger stimuli, such as a nearby dynamite blast, a car horn, or a low-flying jet or helicopter. On two occasions jays gave *Shook's* when chased or harried by robins (*Turdus migratorius*) which were vigorously defending their nest areas. The robins desisted after the *Shook's*. *Shook's* were commonly given by both male and female jays when driving other jays from the vicinity of the nest.

INTEGRATION WITH OTHER BEHAVIOR

A relatively high level of agonistic arousal in jays giving the *Shook* was indicated by (1) the loud, vigorous manner in which the call was delivered; (2) the frequent use of the call in flight (whether chasing or escaping), (3) its use in Aggressive Sidling and (4) in aerial fighting; and (5) the high modal crest angle (70 degrees).

The secondary role played by *Shook's* in supplanting and in other aggressive encounters which were usually predetermined by the dominance hierarchy suggests that in aggressive "confidence" the call was intermediate between the Musical (male) and Rattle (female) and the *Wah* (both sexes). This is discussed in more detail below, in the section entitled Integration of Agonistic Behavior.

BEHAVIOR ELICITED BY SHOOK'S

The varied responses observed to be elicited by *Shook's* indicate that no specific behavior pattern other than perhaps increased awareness or arousal, was released by the call. The most commonly observed responses in birds whose behavior suddenly changed on hearing *Shook's* revealed an increased consideration for their own safety. Low-intensity responses were as follows: temporary cessation of an activity such as Wing-spreading, mobbing, or picking up sunflower seeds, and an appearance of increased alertness shown by raising of the head and turning it from side to side, elevation of the crest, "freezing," or crouching. More commonly, when a series of loud *Shook's* was heard by jays foraging on the ground or on a picnic table, they almost all immediately flew up into the eucalyptus trees. On one occasion, rapid twisting and turning, zigzag flight through an oak canopy was observed, such as might be used in escaping from an accipitrine hawk. Another time, a jay which had been perched atop a tall eucalyptus tree immediately dove down into

the much thicker foliage of a coast live oak. Similar escape reactions of varying intensities were also observed to be given when hunting accipiters were in the area; *Shook's* were commonly given by jays suddenly surprised by an accipiter.

In other cases, however, *Shook's* did not elicit the escape response associated with accipiters or unknown dangers, but instead elicited responses oriented to the calling jay. *Shook's* were the most common call given during Aggressive Sidling, but no change in behavior was ever observed to be associated with hearing the call then. In other contexts, when changed behavior was observed, location of the hearer and the caller in relation to their respective territories was sometimes a deciding factor in the behavior subsequently observed. A female collecting nest material near her nest performed Wing-spreading when *Shook's* were heard nearby. When a male outside his territory heard *Shook's*, he first flew back into his own territory and then performed Wing-spreading. A male on a picnic table outside his territory waited at a distance for the dominant male to leave the bait; but when the dominant male gave *Shook's*, the waiting male quickly flew back to his own territory. Another male near a nest not his own quickly returned to his own territory on hearing *Shook's*. Since *Shook's* were the most common calls given by jays chasing away intruders, it is possible that the calls contributed to causing the intruder to leave; but in these cases and in supplanting, the effects of visual stimuli could not be distinguished from those of vocal stimuli.

Another commonly observed response to the hearing of *Shook's* from a distance was to answer them, usually with more *Shook's* but sometimes with another call. One jay initiating the *Shook's* might in this way cause the hills to resound with the calls of many other jays answering one another. These jays seemed to be on their own territories when calling, and the total effect was in some ways similar to that of the answering of songs in more typical songbirds.

The responses to hearing *Shook's* were basically of two general types: (1) accipiter-oriented, in which a jay flew to safe cover; and (2) jay-oriented, in which the jay flew to his own territory or toward the intruder if within his own territory. Therefore, it is reasonable to suspect that the hearer could tell from the way that the call was being given something about what had elicited it. During the latter part of the field work I felt that I could detect qualities of abruptness, loudness, and brevity in calls elicited by accipiters which were not present generally in *Shook's* elicited by other means; and on the few occasions when it was possible for me to test my recognition of this variant I found that on hearing these calls I could indeed find an accipiter nearby.

In the scrub jay a similar situation was definitely found to exist in the population at the Hastings Reservation. One call ("*whew*") was used in many other contexts, but when given in a special way (abruptly, loudly, with three or four in a phrase, and followed by silence) it could almost invariably be followed by the discovery of a hunting accipiter. Other jays hearing the call probably also recognized this variant as indicating an accipiter, since they reacted by precipitously plummeting for the nearest cover.

It is interesting to note that the *Shook* of the Steller's jay and the "*whew*" of scrub jay are the calls which bear the closest interspecific resemblance in their

sound, were used in similar contexts, and were both modified by abruptness, loudness, and brevity in response to hunting accipiters.

TEE-AR

The *Tee-ar* is well known to field ornithologists because of its resemblance to a scream of the red-tailed hawk. Both male and female jays have been seen giving it; however, it was far more commonly given by males than females, being given by females in only 2 of 39 instances in which the sex of the calling bird was recorded (table 2). Juveniles have been observed giving the call in August.

FORM

The *Tee-ar* was characterized by a clear, whistled quality and a slow, downward slurring for an interval on a musical scale of approximately a sixth. It was usually delivered slowly and singly.

POSTURE

The *Tee-ar* was observed to be given by jays in normal postures, with their heads thrust forward 1-2 cm. One jay was seen giving the call while flying toward the observer and turning its head from side to side. The modal crest angle in a group of 42 observations was 70 degrees, with 84 per cent of the observations at 60 degrees or more (fig. 8). Although *Tee-ar*'s were frequently heard, they were commonly given from concealment; hence, visual observations of calling jays were comparatively few in number. The data in table 14 show that Wing-flicking and tail-spreading did occur with *Tee-ar*'s, but were not characteristic. Tail-flicking was observed in more than half of the cases.

CONTEXT

Seasonal frequency.—Actual counts of the number of individual *Tee-ar*'s heard in the study area on the regular field trips are summarized in table 12. The data show that *Tee-ar*'s were more frequent in March than in April both in 1959 and in 1960. This is indicated both by the number of calls per average composite ten-hour period and by the percentage of days on which *Tee-ar*'s were heard. Furthermore, in 1960 the frequency of *Tee-ar*'s declined from a peak in February through March and April. In contrast, *Too-leet*'s were more common in April than in February or March, and all other calls were more frequent in March and early April than in February (fig. 1). This supports the general impression gained in the field that *Tee-ar*'s reached a peak in conspicuousness and absolute number earlier in the spring than did the other calls. Aside from this difference, the seasonal distribution of *Tee-ar*'s was generally similar to that of the other calls, with a peak in the preincubation months, a decrease during incubation and molting, an increase during the fall, and a low during the winter.

The difference between the years 1959 and 1960 is discussed above under the topic of the seasonal frequency of the *Too-leet* call.

Agonistic situations.—Although the *Tee-ar* was not employed in courtship, neither was it often used in the more common agonistic contexts. As shown in

table 21, it was used in only 3 of 108 instances of calling during Aggressive Sidling. In all kinds of aggressive encounters between banded individuals which were not in groups, the call was used on only 2 of 432 occasions by males (table 16), and on none of 107 occasions by females (table 17). It was not used at all in fighting, chasing, or mobbing (table 21); nor was it used by dominant males when arriving at a picnic table occupied by one or more other jays (table 18).

In the most frequently observed context, the calls seemed to be given at the observer and usually from concealment, or at least from a safe perch high in a tree much farther away than if the jay were mobbing and giving *Wah's*. The jays giving these *Tee-ar* calls had either been surprised by the observer as he walked along a trail or were watching him as he was placing sunflower seeds on a picnic table or getting out of his car. Hence, they were rather unnatural situations to the extent that the calls were a reaction to man.

The situations in which *Tee-ar's* occurred naturally were difficult to categorize. On only three occasions was the call obviously given at other jays, and these were during Aggressive Sidling. Usually, the stimulus eliciting a *Tee-ar* was difficult to identify, because of the practice of giving the call alone, from concealment, and at a considerable distance from any possible stimulus candidates. It was occasionally given by birds going to or from their nests. On two occasions it was given as a red-tailed hawk flew over low. And once it was given by a jay standing inside an unsprung trap.

INTEGRATION WITH OTHER BEHAVIOR

A high level of agonistic arousal in jays giving the *Tee-ar* is indicated primarily by the high level of crest erection. The rarity of this call in fighting, in Aggressive Sidling, in other aggressive encounters between jays, and in mobbing neither supports nor precludes such an interpretation. The rarity of the call in temporal proximity to actual attacks suggests that NBM's for attack were not dominant. The high frequency of calling from a distance or from concealment, especially when the calls were given toward man, suggests that NBM's for avoidance (or escape) were dominant. However, *Tee-ar's* were usually associated with an approach toward man or a reluctance to leave in his presence, rather than with escape or simple avoidance, which were usually carried out silently. Generally, an element of alarm or alertness seemed to be present in all instances.

BEHAVIOR ELICITED BY TEE-AR'S

The only detectable change in behavior in jays just after hearing *Tee-ar's* occurred when they answered them using *Tee-ar's* also. A whistled imitation of a *Tee-ar* invariably caused naïve, hand-raised Steller's jays several weeks old to "panic" and attempt to escape or hide in a corner of their cage.

SQUAWK

The Squawk was heard only rarely, but it was more consistently identifiable with a readily identified agonistic context than any other call. It could be syllabified as "*cack*," "*awk*," or "*ack*," but was of variable form. It was usually loud and noisy, and was rarely repeated. The call was almost invariably given in flight

when the jay was being closely pursued or was diving within several inches of a great horned owl. Usually it was not given unless body contact had just been made or was suddenly imminent. For instance, it was given by a jay who had just been pecked in mid-air by the chasing jay. And it was given by jays who were struck by Western pewees and robins defending their nest areas. When given during the mobbing of owls it was, of course, associated with *Wah*'s, and at times sounded like an exaggerated, explosive form of the *Wah*.

OTHER VOCALIZATIONS

Various other vocalizations were occasionally heard in the study area. Some of these might be considered extreme variations of the calls previously discussed, and possibly some were peculiar to certain individuals, although their rarity precluded verification of this possibility. They are described because they indicate something of the versatility of the jays' voice and because of their relationship to mimicry, and to individual, local, and geographic variation in voice. They were so uncommon that any important functional role seemed unlikely.

PIP

On April 6, 1958, while I stood directly under the nest that O-RXR and MO-MXV were building, one of them gave a series of ten to fifteen nuthatch-like *pip*'s for one or two seconds. A possible variation of the same call was heard on March 21, 1959; MO-MXV went to the nest tree and made a sound which was just like that of a eucalyptus branch bending in the wind (*pip—pip—pip*, etc., at the rate of five or six per second). On April 3, 1959, XRR-RV was also seen giving a series of *pip*'s. Although I have no other records of the call by banded birds, at a few other times when the call was heard the callers were out of sight but within the areas normally frequented by MO-MXV and XRR-RV.

CHIRP

On April 5, 1959, while singing after having fed a fully developed juvenile, XOY-YO interspersed a number of loud clear notes sounding like "*chirp*." The same call had been observed several times the preceding spring in MR-WOX, which repeated it at the rate of three per second in long series, evidently by himself. It was often heard coming from the area frequented by MR-WOX, but the caller was only seldom seen. No other individuals were recorded giving *chirp*'s.

MEOW, EERT

On September 2, 1958, female XWW-RGW was seen giving nasal "*me, me, meow*," a very catlike sound. On the same day, a lone jay partially hidden in the leaves gave a series of high-pitched calls sounding like "*eert*," each one being down-slurred and ending abruptly. These two calls were never heard again, although XWW-RGW was resident in the study area.

SQUIRREL CALL

On November 13, 1959, I heard a nasal, down-slurred call which I at first assumed to come from a scolding fox squirrel (*Sciurus niger*); it was difficult to believe

that it was coming from male O-RXR until I saw his bill open slightly with each call. The calls were given at the rate of about one per second. This was the only record of such a call from the study area. However, on August 4, 1957, on the Hastings Reservation, Carmel Valley, a series of low, harsh notes ("scow" or "scoff") which seemed a good imitation of the gray squirrel's (*Sciurus griseus*) scolding notes was heard from a Steller's jay. In both cases the observer's presence seemed to have elicited the calls and there were no squirrels in sight.

LOCAL VARIATIONS

No attempt to study local variations in vocabulary was made, but experiences in the course of a few trips for other purposes to various areas in the Coast Range indicated that such variations existed. Although the syllabifications of randomly observed calls described here are to a degree subjective and cannot be used in objective comparisons with the descriptions published by other authors, they nevertheless represent real differences heard in the field, and as such deserve mention. The differences which were noted were generally in those calls with a whistled or musical quality and with phrases of a few notes. No differences were detected in the harsh, noisy, single-syllable calls.

An indication of local dialects in jay calls has already been mentioned in the discussion of the *Too-leet*, in which it was shown that the call was essentially restricted to jays in the southern half of the study area and was not recorded from jays in the northern half nor heard from other populations. Individual differences in the Musical which could become the basis for local population differences were shown in table 13 and discussed earlier. A few other geographic variations not heard on the study area will now be mentioned.

At the Hastings Reservation on many days in July and August, 1957, a call was heard from several individuals which has not been heard at any other locality. It seemed to be characteristic of the local population. It consisted of a loud, down-slurred initial note, a modification of the *Wah*, followed by a series of normal *Wah*'s, usually three; and it could be represented as "*cleo-crack-crack-crack*." Sometimes it seemed to be elicited by the presence of the observer.

Just a few miles south of Indian Camp, in Strawberry Canyon, Berkeley, Steller's jays were heard on two occasions giving a call which was never heard elsewhere. It resembled a combination of *Tee-ar* and *Too-leet* in both tone quality and phrasing, and could be expressed as "*tee-ar-o-leet*," the initial phrase sounding like a *Tee-ar* with the usual deflection in pitch, and the terminal phrase containing a two-note sequence with the last note slightly higher than the lowest part of the sound "*tee-ar*." More than one jay was heard giving the call, which was repeated many times.

Similarly, two calls distinctly different from anything heard in other populations were heard in April, 1957, on Mount Diablo, about 20 miles east of Indian Camp. These also had several notes widely separated in pitch and were of a clear, liquid tonal quality. One could be syllabified as "*ee-yo-rk*," with the first note the highest and the second the lowest; the other, with similar intonation, as "*pip-to-it*," perhaps a variant of the same call. Many different calls have been described in the literature, and although some of the differences are merely

subjective, it seems probable from the descriptions that some of these calls also represent individual or local variants analogous to the ones discussed here.

MIMICRY AND LEARNING OF CALLS

Unlike the European jay (*Garrulus glandarius*), the Steller's jays of the Indian Camp populations were only rarely observed in interspecific mimicry. The calls described above which resembled a scolding squirrel, a nuthatch, and a eucalyptus limb creaking in the wind, could be interpreted as mimicry, but these were the only such records in the entire study. The *Tee-ar* might be considered an imitation of a cry of the red-tailed hawk, but it was heard much more commonly than were the cries of the hawks, and it seems as likely that the jays learned it from one another as from the hawks, at least in this locality. The *Tee-ar*, or hawk scream, is widely mentioned in the literature and probably occurs over much of the range of the jay.

Close listening to the phrases employed in the Song might reveal some that were copies from other species, but only suggestions of this sort of mimicry have been heard thus far.

Mimicry of the call of a loon has been reported for the Steller's jay (Munro, 1935). And a call "that sounds like a weak, harsh imitation of the *wake-up* of *Colaptes auratus*" was also noted (Batchelder, 1885).

SEASONAL CHANGES IN FREQUENCY OF VOCALIZATIONS AND ASSOCIATED BEHAVIOR

The occurrence of a peak frequency of various vocalizations in the spring followed by a decline in early summer, and then a second but smaller peak in late summer followed by the low during the winter, is shown in figure 1 and table 12. Figure 1 is based upon impressions of the frequency of each type of call or behavior pattern recorded immediately after the observation period. The presence or absence of the behavior patterns was objectively recorded, but their frequency during the observation period was estimated on a scale from 0 to 4. In order to reduce the dangers of subjective estimation, I chose two calls, *Tee-ar* and *Too-leet*, which could be easily counted during the observation period. Since each *Tee-ar* and each burst of *Too-leet*'s was recorded objectively, these records (table 12) served as a check on the general pattern of the more subjective data in figure 1 and partially verified their validity.

Although no attempt was made to correlate these changes precisely with events of the gonadal cycle and climate, a general correlation with reproductive activities may be drawn. The maximal frequencies in the spring occurred during the period when most paired jays were engaged in courtship and when territorial defense was strongest, but prior to the period of nest building.

Because the data in figure 1 and table 12 are for populations rather than individuals or pairs, the differences between prenesting and incubation periods are smoothed out. In other words, the presence in the population of pairs whose first nesting attempt had failed, and of unpaired jays, and also the lack of synchrony between normal adult pairs in the onset of the reproductive cycle, obscured the sharpness and extent of the change in behavior which occurred when nesting and

incubation commenced. The relative quietness of jays during nesting is a commonplace observation of many amateur students of birds.

For the population as a whole this quietness in the breeding season was most conspicuous approximately from mid-April until July. Correlated with decreased vocal behavior at this time was a preoccupation with care of the young. The rise in vocal activity in the late summer was correlated with a decrease in parental behavior, with the increased wandering of postbreeding jays, and with their accumulation in favorable areas, such as Indian Camp. The contribution of the young of the year to the increased vocal activity in late summer was relatively small, because breeding success was almost nil and because Rattles, Musicals, *Too-leet's*, *Tee-ar's*, *Ow's*, and Growls were rarely if ever given except by adults. First-year jays did, however, contribute to the late-summer increase in frequency of *Wah's* and *Shook's*. Unexpectedly, the period of greatest vocal activity in late summer coincided roughly with the middle of the period of molt, which was heaviest in August and late July.

The period of lowest vocal activity, from November to January, was correlated with cold weather, with relative scarcity of food, and with a low population density due to the exodus from the study area in October of most of the unpaired jays. The brief peak of activity in December, 1959, was the result of a rare chance event, and is not typical of that month. For a period of several days in December, 1959, a female jay had lost her mate. Then another male began courting her, with the result that much vocal activity occurred for two or three days in connection with this unseasonal courtship. The neighboring pairs were also stimulated to greater vocal activity at this time. After these few days, vocal activity dropped quickly to the normal low level characteristic of the winter.

Since in figure 1 the number of observations for each call is approximately the same, a crude estimate of the relative abundance of each call may be obtained by comparing the number of days in the year on which each call was not heard. In order of increasing frequency of days of nonoccurrence in about 175 observation periods, the calls are arranged as follows: *Shook* (1 day), *Wah* (1), Rattle (15), Musical (23), *Tee-ar* (26), *Ow* (75), Growl (77), and *Too-leet* (83). This sequence corresponds to the impression in an average two-hour period in the study area, of the comparative frequency with which each call was heard.

Some differences in the seasonal patterns of frequency between the various vocalizations exist, but explanations for most of these differences are not readily available. For example, it has already been noted (in connection with the seasonal frequency of the *Tee-ar*) that the frequency of *Tee-ar's* reached its peak in February, earlier than the peak frequencies of other calls.

Also it may be seen in figure 1 that the distribution patterns for the Rattle and the Musical are quite similar, and together differ in minor ways from the patterns for all other vocalizations. Similarly, the patterns for *Wah* and *Shook* have much in common; and both differ from the Rattle and the Musical in their continuation of the late-summer plateau of high frequency into August and September. Since *Wah* and *Shook* were the commonest calls of first-year jays and of others without territories, a reasonable explanation for this difference might be the beginning of more

frequent vocalizations by young jays, the effect of which was diminished in October and late September by the general exodus of jays without territories.

Another difference in seasonal distribution may be seen in the *Ow*. Figure 1 shows that the spring rise in frequency began about two weeks later than in the other calls and reached its peak when all other calls except the Rattle and the Musical had begun their decline. No explanations for this difference and for some of the others which close inspection of figure 1 reveals are apparent.

INTEGRATION OF AGONISTIC BEHAVIOR

PATTERN OF ORGANIZATION OF AGONISTIC BEHAVIOR IN THE STELLER'S JAY PREDISPOSING AND ELICITING FACTORS FOR AGONISTIC BEHAVIOR

Since the integrative mechanisms of agonistic behavior cannot be studied in isolation from the stimuli which activate them, it is necessary to deal with both together.

Activation of the series of behavior patterns in the Steller's jay correlated with increasing agonistic arousal bears a relationship to a number of stimulus factors in addition to the intensity of resistance of the opponent. These may be grouped into two classes: (1) factors which predispose toward a higher level of agonistic behavior, and (2) factors which immediately elicit higher levels of agonistic behavior.

Among the factors which may determine the predisposition of a jay toward agonistic behavior are: (1) location in respect to its territory, (2) previous experiences of the jay in aggressive encounters with particular jays (this factor in part determines the significance of location), (3) phase of the gonadal cycle, and (4) goal valence to the jay of the object of the encounter (determined by degree of hunger, thirst, etc.) or need state.

These factors by themselves do not elicit agonistic behavior, but generally require the presence of an eliciting factor also. Factors 1 and 2 work together, in the same sense that the success of a jay in previous encounters with particular individuals at a particular location determines the jay's predisposition to attack or escape that individual at future times at the same location. The prenesting behavior of the Steller's jays, which is correlated with the gonadal cycle, is characterized by increased wariness outside their territories and by an increased probability of display or unprovoked attack at intruders within their territories. Except in the breeding season, a jay usually supplanted other jays in its territory only when there was a specific goal, such as a food source. While the dominant jay was storing a load of sunflower seeds, other jays were free to take seeds from the same source. Thus the attacks of dominant jays were largely contingent upon their predisposition to attain a goal. When that predisposition was absent, or if the jay was otherwise occupied, attacks did not occur. All of these factors which may predispose a jay toward agonistic behavior seem to facilitate agonistic behavior at any level of arousal. At least the first three may facilitate either attack or escape in appropriate situations.

Among the factors which may immediately elicit a higher intensity of agonistic behavior are: (1) resistance of the immediate opponents; (2) aggressive behavior

of other jays, especially calls; (3) actions of other species (e.g., owls, cats, man); and (4) miscellaneous noises and movements, such as jets, helicopters, buses, wind, and the rustling of leaves. Two or more of these factors in addition to the predisposing factors may combine to determine the level of agonistic behavior.

DIFFERENCES BETWEEN SEXES IN AGONISTIC BEHAVIOR

Male jays were generally dominant to and more frequently aggressive than females. In dominance hierarchies based on supplanting encounters observed at picnic tables, males ranked above females with few exceptions. Males also participated more frequently in supplanting encounters than did females; on 11,410 occasions when a color-banded jay was recorded as a participant in a supplanting

TABLE 23

COMPARISON OF CREST ANGLES IN MALE AND FEMALE STELLER'S JAYS DURING SUPPLANTING ENCOUNTERS AT T7 IN WHICH THE ATTACK WAS BEGUN ON THE TABLE AND NO INCREASE IN CREST ANGLE WAS OBSERVED (SIMPLE SUPPLANTING)

Individuals	Degrees of elevation of crest										Total	Mean
	0	10	20	30	40	50	60	70	80	90		
10 males.....	7	17	34	50	12	5	7	1	1	..	134	27
Female XW-WW.....	.	1	5	18	.	1	..	.	1	..	26	30
Female MVM-VXM.....	6	4	..	1	11	6

NOTE: Data are actual numbers of observations, not percentages.

encounter, the percentage of females recorded ranged from 6 per cent of 1,786 occasions in May to 44 per cent of 572 occasions in December and January, with an average of 24 per cent for all months combined. Females were accordingly less successful than males in supplanting encounters involving both sexes, winning 606 and losing 2,185 in the same period.

The lower frequency of encounters and especially of wins in females than in males, is reflected in the sex ratios of the calls listed in table 2. In all calls which were given by both sexes, the proportion of records for males was much higher than for females. Except for Song and Gutturals in some contexts, all the calls were given primarily in agonistic contexts; and since males more frequently participated in supplanting than females, they had more frequent opportunities to use the calls. Males also participated more frequently than females in Aggressive Sidling (95 per cent of 95 observations) and in aerial chasing (85 per cent of 27 observations). *Shook's* were the most common calls in the latter two contexts, a fact which correlates with the low percentage (12 per cent) of *Shook's* recorded for females. In contrast, the percentage of observations of *Wah's* by females was much higher, 44 per cent. *Wah's* were more commonly used in mobbing and other situations in which supplanting, chasing, and Aggressive Sidling did not occur, and in which participation by both sexes was more nearly equal.

Despite the lesser success and frequency of females in aggressive encounters, in quality their behavior was not noticeably different from that of males, except for the calls which were restricted to one sex, such as the Musical and the Rattle. In

table 23 it is shown that the crest angles during supplanting were generally similar in males and a female, although another female was anomalous. In table 24 the crest-angle distributions during *Wah's* in males and females are shown to be similar, with means of 60 and 59 degrees respectively; however, the modes differ by 10 degrees. Although the data for other calls were not sufficient for such a detailed comparison, no indications have been found of differences between the sexes in crest-angle distributions for a given call or other activity. Therefore, no important differences between the sexes in the organization of agonistic behavior are apparent, except in frequency and success and in the Rattle and the Musical, which essentially correspond to each other in the ways in which they were used. These differences could be theoretically accounted for partially on the basis of an average

TABLE 24

A COMPARISON OF CREST-ANGLE DISTRIBUTIONS IN FOURTEEN MALE AND NINE FEMALE STELLER'S JAYS DURING WAH'S, IN THE PERIOD SEPTEMBER, 1958-APRIL, 1960, INCLUSIVE

Sex	Degrees of elevation of crest											
	0	10	20	30	40	50	60	70	80	90	N	Mean
Male.....	..	2	3	7	6	8	22	32	15	4	99	61
Female.....	3	6	13	11	29	24	14	..	70	59

NOTE: Data are expressed as percentages of N.

difference in androgen level between the sexes, higher levels of androgen in males possibly causing lower thresholds for agonistic behavior than in females. The larger size of males may also be important in their more frequent success in supplanting females.

BEHAVIORAL EVIDENCE FOR THE CONCEPT OF AGONISTIC AROUSAL

By "agonistic arousal" is meant the activation of the neural substrate necessary and sufficient for agonistic behavior. In this study, agonistic arousal may be recognized only by behavioral parameters. In calibrating the scale of agonistic arousal it is first necessary to establish a series of behavioral reference levels. Because the act of aerial fighting probably represents the highest intensity of muscular action and physiological readiness for action, it will be used to represent the extreme form of agonistic behavior and therefore the highest level of agonistic arousal. Aggressive Sidling is the behavior pattern which usually follows aerial fighting, or may substitute for it; consequently it will be interpreted as representing a level of agonistic arousal just below that of aerial fighting (Criterion 2B in table 25). On the other end of the scale, sleep and rest may be interpreted as representing the lowest level of agonistic arousal, with normal foraging and feeding behavior representing a slightly higher level. At an intermediate level is the Wing-spreading accompanied by Guttural notes. The correlation of these levels with the degree of resistance of the opponent during supplanting has been discussed above, in the section entitled Crest Movements, and is shown in table 11.

The existence of a common factor in the integrative system for a variety of types of threat behavior is suggested by the following considerations: (1) Increasing

the intensity of the family of stimuli which constitutes the resistance of the opponent leads to a recognizable series of behavior patterns, from Wing-spreading, through Aggressive Sidling, to aerial fighting. (2) The angle of the crest is directly correlated with both the resistance of the opponent (table 11) and the series of behavior patterns just mentioned. (3) The various stages of this series are characterized by particular vocalizations, which are also correlated with crest angle.

TABLE 25

CRITERIA FOR INTERPRETING THEORETICAL PRESENCE OF ACTIVATION OF A NEURON POOL
CONCERNED WITH A PARTICULAR FUNCTIONAL GROUP OF BEHAVIOR PATTERNS
FROM OBJECTIVE OBSERVATIONS OF BEHAVIOR

Level of inference	Criteria of activation of population of neurons	Example for attack	Example for Steller's jay
1. Primary	Occurrence of the definitive act	Actual attack	Supplanting attack; combat
2. Secondary	A. Occurrence of isolated elements of definitive act	Incomplete attack actions	Pecking; rapid approach
	B. Occurrence of acts temporally associated with definitive acts	Threat display, strong	Aggressive Sidling
	C. Occurrence of environmental context associated with definitive act	Trespasser within territory	One jay near another's nest
3. Tertiary	A. Occurrence of isolated elements of secondary-level acts	Incomplete threat display	Displacement bill-rapping; <i>Shook's</i> (elements of Aggressive Sidling)
	B. Occurrence of acts temporally associated with secondary-level acts	Threat display, weak	Wing-spreading
	C. Occurrence of environmental contexts associated with secondary-level acts	Territory border	Where Aggressive Sidling occurs

NOTE: The dependability of these criteria decreases with increasing level of inference. Tinbergen's (1959) criteria (a) ("elements of recognizable motor patterns"), (b) ("time scores"), and (c) ("compares the external situations") correspond to my criteria 2A and 3A, 2B and 3B, and 2C, and 3C, respectively.

(4) The series appears to be one of increased vigor and exertion behaviorally and, therefore, is probably accompanied by increases in the physiological parameters normally associated with increased activity, such as heart rate, blood pressure, and localized vasomotor effects. The striking correlation between the factors just mentioned supports the interpretation that activation of a single, large population of neurons may be a common factor in the integration of all the behavior patterns indicated above into the functional pattern which has been observed.

RELATION OF ATTACK AND ESCAPE TO AGONISTIC BEHAVIOR

General.—The concept of agonistic arousal is not sufficient in itself to explain all of the behavior observed in the Steller's jay. Although all of the behavior patterns which have been shown to be agonistic can be fitted into a linear sequence using the parameter of mean crest angle, such a procedure ignores the variety of

factors which cause differences in behavior at the same crest angle. Examination of any of the frequency distributions of crest angles (figs. 3 through 8) shows that the same activity may occur at a variety of crest angles, and that a variety of activities may occur at the same crest angle. At one crest angle a jay may attack, escape, advance, retreat, call, remain silent, or display in a variety of postures. Therefore, factors influencing variation in behavior at the same level of agonistic arousal must be considered if we are to gain further insight into the integration of the total complex of agonistic behavior.

Since virtually no single behavior pattern has been observed in which each performance is invariably characterized by a predictable crest angle, the integrating mechanisms for the respective behavior patterns must differ from each other in more than the one theoretical parameter of intensity of activation. Therefore, the integration of each behavior pattern is not the property of only one population of neurons for agonistic behavior but of a number of populations. The problem, then, becomes one of identifying and describing the properties of the additional hypothetical populations in terms of observed behavior.

The discrimination and identification of higher levels of integration (those affecting a wider variety of behavior patterns) cannot be done entirely on the basis of the observed patterns of effect or action of individuals. The context in which the actions occur is also important, for it supplies the immediate eliciting sensory input and determines functional consequences of the acts themselves. It is generally accepted that the central nervous system (CNS) is organized on the basis of functional systems. For instance, there is fairly discrete localization at various structural levels in the CNS for such functional systems as vision, audition, and other sensory systems, voluntary muscle control, postural reflexes, blood pressure, and respiration. It is therefore to be expected that the neural mechanisms for some of the more basic behavioral functional systems may also have structural localization to some extent. So it is logical to select groups of behavior patterns with a common function and to examine their components, on the assumption of a common structural localization. Threat behavior may be one such functional group. Behavior patterns relevant to attack and escape constitute two other possible groups.

In all agonistic behavior the nervous system must somehow effect a compromise between the behavior patterns which are directed toward the avoidance of and escape from danger and those which are directed toward the attainment of a dangerous goal. Some of these goals are the attainment of food or a mate in the face of competition, defense of an area, and defense of the nest, eggs, and young. In pursuit of some of these goals, fighting or threatening may frequently be employed. Hence, it has commonly been assumed that in most agonistic behavior there is a conflict between the NBM's for escape and those for fighting or attack, although other types of conflict are also possible, depending on the situation. Other authors have found it convenient to interpret agonistic behavior in various species in terms of the intensity and balance of the conflicts between attack and escape NBM's which were inferred to accompany the behavior in question (e.g., Tinbergen, 1959).

The criteria listed in table 25 will be used in an attempt to determine the balance

or dominance of attack and escape NBM's in the principal agonistic behavior patterns of the Steller's jay.

Relative dominance of attack and escape NBM's in some displays.—In Aggressive Sidling the lateral and parallel orientation of displaying opponents suggests a balance between attack and escape NBM's; this orientation represents a compromise between facing the opponent in frontal position, a component of actual attack, and facing away, a component of escape (Criterion 2A). The typical absence of advancing or retreating by the opponents may be similarly interpreted (2A). The employment of Aggressive Sidling between males at their mutual territorial boundaries also suggests that the attack and escape NBM's are rather evenly balanced (2C). That Aggressive Sidling sometimes precedes and frequently follows actual fighting might be interpreted to indicate a dominance of the attack NBM's (2B), although the change in behavior of the opponent may also be important in this case.

Since *Shook* is the most common call given during chasing (table 21) and the second most common call during supplanting attacks (table 20), it could be interpreted as an indicator of dominance of the attack NBM's (2A). That *Shook* is also the most common call in Aggressive Sidling (table 21) suggests that the attack NBM's are dominant in that activity also (2A). To complicate the analysis further, however, *Shook*'s are also the most frequent call during escape from banding operations (table 22); hence, their occurrence in Aggressive Sidling would indicate a dominance of escape NBM's (2A).

Therefore, three arguments agree in suggesting a balance between attack and escape mechanisms; two suggest dominance of the attack mechanisms; and one suggests dominance of the escape mechanisms. Consequently, the display is difficult to characterize on the basis of attack and escape NBM's alone. However, the more direct and easily observed indicators, such as the jay's failure to advance or retreat at his territorial border, suggest a balance between attack and escape NBM's. And the indirect criteria which rely on vocalizations as indicators, and on proximity to actual attacks or escapes, are susceptible to alternative explanations, as will be shown. Also, the display may cover a range from dominance of the attack NBM's at some times to dominance of the escape NBM's at others.

In Wing-spreading, which generally is accompanied by Guttural calls, the orientation of the displaying jay is frontal, toward the opponent, which suggests dominance of the attack NBM's (2A). However, the display is given at long range (e.g., 5–50 feet) from the opponent, rather than at short range ($\frac{1}{2}$ –2 feet) as in Aggressive Sidling, and the orientation at such a long distance would seem less important as an indicator of attack NBM's. The spreading of the wings has the appearance of a movement which has become evolutionarily specialized for a display purpose; thus, its components cannot be interpreted as unmodified elements of the motor patterns of attack or escape mechanisms. Since the wings are used in attacking and escaping, and in begging for food by juveniles and adult females, and are also slightly spread when the bird is perched in very warm places, the evolutionary derivation of the display is not clear and is of no use in determining the dominance of attack or escape NBM's. The characteristic infrequency of advance or retreat during the display suggests a balance of attack and escape NBM's (2A). The frequency of the display in territorial border encounters between pairs,

suggests a balance of attack and escape NBM's at those times (2C). Since fights, chases, and supplanting attacks were not commonly temporally associated with Wing-spreading, they do not supply evidence for a dominance of either attack or escape NBM's (2B). Consequently, there is not a good argument for conspicuous dominance of either the attack NBM's or the escape NBM's. Furthermore, the evidence cited under the discussion of Wing-spreading in the section on Postures and Movements suggests that because of the heterogeneity of the contexts in which it occurs Wing-spreading cannot be characterized simply by one combination of two groups of behavioral NBM's, but is correlated with a wider variety of behavioral mechanisms.

Attack and escape NBM's in some vocalizations.—Of the criteria in table 25, only Criterion 2B is useful in assessing the strength of attack and escape NBM activation during vocalizations. Criterion 2A cannot be used, because no vocalization is necessarily a part of the definitive acts of attack or escape. Criterion 2C is of little use, partly because the spatial contexts of the different vocalizations are largely the same; all are most common within the caller's own territory. Therefore, by elimination, only the criterion of temporal proximity to the definitive acts of attack and escape (2B) is useful, with but few exceptions.

In singing jays which were not engaged in courtship, activation of escape NBM's was indicated by the fact that the Song was commonly elicited by the approach of a person (2C). Since the singing jays did not leave in response to danger, another behavioral NBM was probably in conflict with the escape NBM's. Neither NBM could be interpreted as being dominant.

A characteristic dominance of the attack NBM's during the utterance of Rattles and Musicals is suggested by their frequent performance before or during supplanting attacks (2B). In this respect Rattles and Musicals differ from Gutturals, which, though given within a similar range of crest angles, are generally dissociated from actual attacks.

A similar comparison may be made between *Shook's* and *Wah's*, for which the modal crest angles are both 70 degrees (fig. 8). In 60 supplantings, *Shook's* were used on 18 occasions and *Wah's* on 6 (table 20). In 33 aerial chases, the attacking jay gave *Shook's* on 5 occasions and *Wah's* on none (table 21). In 9 aerial fights *Shook's* were given on 7 occasions and *Wah's* on 2 (table 21). And in 154 cases of a dominant jay's arrival amongst a group of subordinates at a picnic table, *Shook's* were given on 53 occasions and *Wah's* on 35 (table 18). These four types of evidence all indicate a generally higher probability of *Shook's* than of *Wah's* accompanying attack (2B). And they suggest that during *Shook's* the attack NBM's are often dominant. It should be noted also that all these situations frequently involve calls given while the bird is in flight or just after alighting.

When the same criterion (2B) is used for estimating the escape NBM's in *Shook's* and *Wah's*, a contradictory interpretation results. Of 22 occasions when calls were given in flight by jays "escaping" from the bander's hand, 17 involved *Shook's*, and 4, *Wah's* (table 22). After jays had alighted from these "escapes," when the escape NBM's might be expected to be less active, or at least not more active, *Wah's* were given on 17 occasions and *Shook's* on 2. When these data are considered alone, the escape NBM's could be interpreted to be generally dominant

in both *Shook's* and *Wah's* (2B), but more so in *Shook's*, because they occurred in closer temporal proximity to the "escape."

To complicate the situation still further, the predominance of *Shook's* in Aggressive Sidling adds the uncertainties which are discussed above for that display to the factors to be considered in assessing attack and escape NBM's. The predominance of *Wah's* in mobbing and in situations characterized by alertness is also difficult to interpret in terms of attack and escape NBM's. A number of interpretations may be considered. (1) Other factors may be more important than the theoretical attack and escape NBM's in the integration of *Shook's* and *Wah's*; or (2), insufficient data may have led to the misapplication of the criteria used; or (3) both.

The first alternative requires one or more integrative mechanisms in addition to the attack and escape NBM's. The correlations between the occurrence of *Shook's* and the act of flying and between the occurrence of *Wah's* and the act of alighting suggest two additional integrative phenomena which could contribute to explaining the observed behavior and which would delegate the attack-escape hypothesis to a level of lesser importance. This suggestion nicely fits the distribution of calls after release from banding, but the data in regard to supplanting attacks were not collected in such a way as to allow a test of it. That it cannot be the whole explanation is apparent, because *Shook's* were commonly given by perched jays also, as in Aggressive Sidling.

In regard to the second alternative interpretation, the misapplications of Criterion 2B, it is pertinent to reconsider the crest angle of some jays thought to be dominated by fear (escape NBM's). These jays, which had been trapped and released into an aviary, hid silently and attempted to escape with the crest depressed when a man entered the aviary; but when they became accustomed to the aviary, their hiding was less intense, *Wah's* were uttered, and the crest was raised in response to the same stimulus of a man entering the aviary. It is reasonable to expect that as the jays became accustomed to the aviary, their fear of a man in the aviary either lessened or was in conflict with a greater confidence or attack NBM activation, which change produced the change in observed behavior. Since jays released from banding also gave *Wah's* with the crest erect in an area to which they were accustomed, it may be argued by analogy (2C) that the escape NBM's were not strongly dominant, as suggested by Criterion 2B, but were reduced or in conflict with another NBM both in flight while giving *Shook's* and after alighting when giving *Wah's*. Consequently, occurrence of an act immediately after escape would not necessarily be a safe indicator of the strong dominance of the escape NBM's if the escape took place within the bird's accustomed home aviary or territory. The usual increase in crest angle and tail-flicking in jays immediately after being supplanted (table 8) may also be explained by a similar hypothesis.

When all factors are taken into consideration, the data favor the hypothesis that *Shook's* may be characterized often by a dominance of the attack NBM's, sometimes by a closer balance between attack and escape NBM's, and sometimes by dominance of escape NBM's. *Wah's* may be characterized by a balance between attack and escape NBM's, but usually not by a strong dominance of either. In addition, the acts of flying and of alighting have an important effect on the inte-

gration of *Shook's* and *Wah's*, as explained above. Therefore, the attack-escape theory is not in itself sufficient to explain the occurrence of *Shook's* and *Wah's*, but must be supplemented by the additional theoretical considerations just mentioned. Furthermore, the criteria used to identify dominance of the escape NBM's conflict in their implications, and one (2B) is probably unreliable for this purpose.

The use of *Too-leet's* in supplanting (table 19) suggests a frequent dominance of the attack NBM's (2B), but the frequent association of *Too-leet's* with Aggressive Sidling (table 19) makes the interpretation of the call in terms of a simple combination of attack and escape NBM's complicated.

Since the *Tee-ar* was commonly given by a jay that was alone, from concealment, and at a considerable distance from the eliciting stimulus, it seems to be less often dominated by NBM's for attack than the other calls given at similar crest angles (*Wah*, *Shook*, *Too-leet*) (2B).

Because of the frequent association of the Growl with aggressive encounters (2B), jays giving this call are probably dominated frequently by NBM's for attack.

GENERAL ORGANIZATION OF AGONISTIC BEHAVIOR

Analysis of agonistic behavior in the Steller's jay has revealed an impressive degree of variability; the behavior is not confined to a few stereotyped displays. A conspicuous feature of crest erection, tail-flicking, tail-spreading, Wing-flicking, and Wing-spreading is their lack of precise correspondence with specific vocalizations and other activities. The use of vocalizations and displays in particular behavioral contexts also shows an impressive amount of variation. Part of this variation results from the difficulty of clearly and discretely categorizing complex behavioral contexts as observed in the field. However, even when this variable is reduced by considering only the correlation between more objectively estimated behavioral parameters, such as crest angle and tail-flicking intensity, the variation is so great that individual observations cannot be interpreted consistently as resulting from interactions of only two unitary behavioral NBM's for attack and escape.

On the other hand, *average* differences in the activation of certain behavioral mechanisms between different behavior patterns could theoretically be expressed by attack-escape NBM interactions. Individual observations, however, may not be interpreted safely from such average characterizations. For example, it does not necessarily follow that because *Musicals* are the most common calls during supplantings, the attack NBM's must always be dominant at other times at which *Musicals* are given. And the high frequencies of *Shook's* during attacks on other jays did not preclude *Shook's* from being also the predominant call during escapes from the hand.

In summary, the distributions of crest angles, tail-flicking, Wing-flicking, and some other characters show that the different vocalizations and displays are correlated generally with different levels of agonistic arousal. Additionally, the differences in use of calls in attack contexts show that the vocalizations are also correlated to some extent with differences in degree of dominance of the attack NBM's. For convenience in discussion, the *Shook*, the *Wah*, the *Tee-ar*, and the *Too-leet* may be considered to have a high level of agonistic arousal, since the crest angles that

accompany them are mostly 60 or more degrees. The other vocalizations may be considered as a somewhat more heterogeneous group according to their crest angles, with low and moderate levels of agonistic arousal (crest angles mostly 50 degrees or lower).

Within the group characterized by a high level of agonistic arousal, the calls differed in their frequency of association with attack. In all attack contexts *Shook's* were conspicuously more frequent than *Wah's* (tables 19, 16, 17, 20, 18). And of the total number of recorded calls of each type, the proportion used in supplanting was higher for *Shook's* than for *Wah's* (table 19). Therefore, in general the *Shook* appears to be characterized by a higher average activation of the attack NBM's than the *Wah*. The same tables also show that the *Shook* was more closely associated with attack than were any of the other calls with a high level of agonistic arousal. *Too-leet* was generally less frequently used in attack contexts than either *Shook* or *Wah*, but of the total number of times that it was recorded, the proportion involved in attacks was higher than the proportion for either *Shook* or *Wah*. However, the number of observations (30) and the unsystematic way in which the observations were recorded, suggest caution in concluding that it represents a higher attack NBM activation than does *Shook* or *Wah*. *Tee-ar* was rarely if ever associated with attack, being given mainly from a distance and from concealment. Therefore, in general the four calls which were given primarily at high levels of agonistic arousal may be arranged in order of decreasing average attack NBM activation as follows: *Shook*, *Wah*, *Too-leet*, *Tee-ar*.

Within the group of vocalizations characterized by moderate or low levels of agonistic arousal, the calls also differed in their frequency of association with actual attack. In all attack contexts, the Musical was the most frequently used call by males, and the Rattle, by females. Gutturals and *Ow's* were relatively infrequent. The percentage of Growls used in attacks, as opposed to other contexts, was greater than comparable percentages for some other calls (table 19); but the number of observations (15) is too small to be reliable, and the call was less frequent than any of the other calls in the same group.

The order of decreasing average attack NBM activation would then be, roughly: Musical (males) and Rattle (females), Growl, Gutturals, and the *Ow*.

In regard to displays, the situation is simpler than for vocalizations. There is one display characteristic of high levels of agonistic arousal, which is Aggressive Sidling, and one characteristic of low levels, which is Wing-spreading. Both are essentially stationary displays and reflect a lack of dominance of attack or escape NBM's. Tail-flicking and Wing-flicking are roughly proportional to the intensity of agonistic arousal, as is crest erection.

NEURAL FACTORS

Since the integration of agonistic behavior in any species can be understood completely only by consideration of anatomical and physiological aspects in addition to the behavioral ones, it behooves the behaviorist working on the problems of behavioral integration to consider the relevant information from these fields. Fortunately, a considerable amount of research work is already available concerning the neural bases of agonistic behavior in the cat. (For a review of the literature

see Hunsperger, 1959.) In addition, work is now in progress on the hen (von Holst and von St. Paul, 1960). Since in the cat, at least, the work till now has concentrated on the localization of behavioral function within the brain, the anatomical basis of agonistic behavior in that species is better known than in any other species. But because it is dangerous to make trans-specific comparisons, let alone trans-class comparisons, between cat and jay concerning neural anatomy and behavior, any insight into bird behavior gained as a result of the research on agonistic behavior in cats must be general and of a highly tentative nature.

The concept of agonistic arousal, as developed for the Steller's jay, has a neurophysiological basis in the cat as follows: The areas in the cat's brain which yield agonistic arousal include, *a priori*, all those which upon stimulation yield agonistic behavior. Although each of these areas (midbrain, hypothalamus, amygdala, and intervening pathways) has special properties of its own and yields rather different types of agonistic behavior, all have in common the property of agonistic arousal as manifested by such signs as arousal from sleep or arrest of other activities at the onset of stimulation, pupilodilatation, pilo-erection, flattening back of the ears, increases in the rate of respiration, increased blood pressure and motor activity, and the occurrence of vocalization.

As in the jay, in which certain general indicators of agonistic arousal, such as crest erection, were found valid no matter what specific form of agonistic behavior occurred, so also in the cat, such general indicators as listed above (e.g., pupilodilatation, flattening of the ears) were found valid to various degrees no matter which area in the brain was stimulated, so long as agonistic behavior of one type or another was elicited. Therefore, in species as different as jay and cat, certain aspects of behavior may apparently be used as indicators of general agonistic arousal and the accompanying activation of the brain regions responsible for agonistic behavior without giving any information concerning what specific region within the zones of the brain for agonistic behavior is most active.

Furthermore, increases in stimulus strength in experiments on the cat were proportional, within limits, to the observed strength of response of these indicators. Therefore, because of the generality of the relationship between strength of neural activation and strength of behavioral response in vertebrate nervous systems, it is logical to infer that the crest and similar indicators of agonistic arousal in the jay are also reflecting in an approximate way the strength of neural activation somewhere within the zones for agonistic behavior in the jay's brain.

It follows from the wide range of agonistic behavior patterns in cat and jay for which these indicators are valid, that attempts to identify them with certain patterns of activation of attack and escape NBM's are dangerous. In the cat at least, there seems little justification for doing so, since the behavioral, anatomical, and physiological bases of these indicators are so well known.

The concept of agonistic behavior as a product of varying degrees of activation of attack and escape NBM's finds little justification from the neurophysiological work on cats. The main obstacles to such a theory thus far are (1) the absence of a known zone for pure attack, and (2) the pattern of spatial representation of escape and defense behavior in the brain stem of the cat. The attacks which may be observed upon brain-stem stimulation are primarily of a defensive character

in response to an object thrust near them, and generally arise from a defensive threat posture. Under different experimental conditions and training procedures, it might be possible to obtain more typical attacks.

The pattern of spatial representation of defense and escape behavior as found by Hunsperger (1956) consists of zones for defense in the midbrain and hypothalamus, surrounded and connected by continuous zones for flight. In addition, flight and defense were obtained in the amygdala and one of its connections to the hypothalamus, the stria terminalis (de Molina and Hunsperger, 1959). The study disclosed several differences between these various areas in the nature of the reaction obtained. Thus hissing was the typical vocalization from the hypothalamus, and growling from the amygdala. From this it can be seen that an anatomical basis exists to explain two of the types of vocalization accompanying agonistic behavior, and that the anatomical picture does not correspond to a pattern of differential activation of attack and escape loci, since it is already known to be more complex than required by the attack-escape theory.

A third neurological finding that is not accommodated by the attack-escape theory in the cat is that so-called "conflict behavior," such as the defense behavior of cats, is typically elicited from a single electrode. It might be argued that the electrode lies between areas for attack and escape, but in fact such "conflict behavior" is elicitable from extensive areas which are known to be surrounded only by a neural substrate for escape, or by regions which yield no agonistic behavior.

In domestic fowl the neural organization of agonistic behavior appears to be possibly closer to that suggested by the attack-escape theory (von Holst and von St. Paul, 1960). First, in contrast to the cat, it was possible to find separate areas in the bird brain which would elicit attack and escape behavior. Secondly, as predicted by the attack-escape theory, simultaneous electrical stimulation, at moderate intensities, of these areas which separately would elicit flight and aggressive pecking (*Hacken*) yielded a compromise behavior in which the hen remained as if clamped to one spot, neither advancing nor retreating. And in another experiment an intensification of the threat display was elicited by simultaneously stimulating a flight locus and an aggressive pecking locus (von Holst and von St. Paul, 1958). Although it is tempting to interpret such data as being in support of the attack-escape theory, the published information on such experiments at present is insufficient to enable one to make a proper evaluation.

In any case, the more fundamental question is, how does the CNS integrate agonistic behavior, not whether or not a particularly simple and pliable theory is neurologically correct. As there is no clear physiological evidence at present which can prove or disprove the attack-escape theory, research could more profitably be aimed toward the exploration of new concepts, with fresh approaches.

SUMMARY

INTRODUCTION

The agonistic behavior of a population of Steller's jays near Berkeley, California, in which 114 jays were color-banded, was studied from March, 1957, through April, 1960. Mated pairs resided in their territories throughout the year. Territories were not strongly defended even in the breeding season.

POSTURES AND MOVEMENTS

The two principal displays were Wing-spreading and Aggressive Sidling. Movements of the crest, wings, and tail are considered separately and in relation to one another and to the vocalizations.

Wing-spreading was characterized by a moderately low crest angle. It was given in a variety of conflict situations not limited to conflicts between attack and escape mechanisms. The hypothesis is proposed that Wing-spreading may have been elicited by a wide variety of inputs or moods, because it had a relatively low threshold.

Gaping and appeasement begging were uncommon and were generally restricted to low-ranking individuals.

Both Aggressive Sidling and Sexual Sidling resembled the lateral display of *Garrulus*, but had fewer components and were, therefore, less specialized. Aggressive Sidling differed from Sexual Sidling in its high crest angle, its frequent association with calls termed *Shook's* rather than Song, and its use as a threat rather than as courtship. Aggressive Sidling frequently followed fights at territorial boundaries.

Erection of the dorsal feather tract, with depression of the crest, was observed only rarely, but it was common in one female which ranked low in the dominance hierarchy and was frequently rebellious.

Displacement bill-rapping and digging were common during Aggressive Sidling and were associated with a high level of agonistic arousal, as indicated by crest angles especially. The type of displacement behavior shown was strongly dependent on the substrate. Displacement behavior graded imperceptibly into normal foraging behavior as aggressive encounters terminated. Bill-rapping is interpreted as derived from foraging movements rather than from the pecking components of attack. The hypothesis is advanced that displacement behavior results from intense arousal of CNS zones in which both threat behavior and the normal form of the displaced behavior are localized.

Tail-flicking occurred most frequently during mobbing and after alighting in a situation causing alertness; the crest was typically erect at these times.

Wing-flicking was correlated with the higher intensities of tail-flicking, which were, in turn, correlated with the higher intensities of crest erection. On the basis of these and other evidences of coordination, the hypothesis is advanced that these behavior patterns share a common population of activating neurons and are differentially activated according to differing thresholds.

The tail could be spread while being depressed, as in slow threatening approaches, or while being flicked upward, as in mobbing. When the tail was not being flicked, the crest was higher when the tail was spread than when it was not.

The angle that the leading edge of the crest made with the bill was used to estimate crest erection. The crest was generally depressed in courtship and courtship feeding. Crest angles were largely independent of the degree of body-plumage erection; but during preening and sun bathing the angles increased in proportion to the degree of body-plumage erection (modes 30 degrees and 60 degrees respectively). When the jay was foraging or storing, with the bill in frequent contact

with the ground, the crest was actively depressed. During more vigorous opening of acorns and during the taking of bait from picnic tables, the crest angle was more variable, and averaged somewhat higher (mode 30 degrees).

The crest was raised primarily in agonistic behavior, being most consistently and fully erected during aerial combat (mode 90 degrees) and Aggressive Sidling (mode 80 degrees). In contrast, during simple supplanting the mode was 30 degrees. No correlation between crest angle and sex of the supplanting jay, rank of the supplanting jay, or rank of the supplanted jay could be found in this type of supplanting encounter. When an increase in angle occurred during supplanting, the modal angles were 20 and 30 degrees before supplanting and 40 degrees afterward. Increases generally occurred only when the opponent briefly resisted or was slow in leaving. Except in certain special contexts, primarily those associated with the lower range of crest angles, the generalization could be made that the extent of crest erection was roughly proportional to the degree of agonistic arousal, which itself was primarily dependent on the resistance of the opponent or other stimuli connoting danger to the jay. This relationship conforms with the general principle of economy of threat display: the intensity of threat display used in a given situation tends to be proportional to the amount of resistance offered by the opponent.

The modes of crest-angle distributions were similarly high for the following activities: alighting alone on a picnic table, supplanting by a direct flight from a distance, high-intensity tail-flicking, Wing-flicking, alighting for the first time after release from banding, alighting after being supplanted, and during the call designated as *Wah*. In all of these activities the modal crest angle was 70 degrees, except for the supplanted jays, in which the angle was 60 degrees. All these activities shared to a great extent the circumstance of the jay's having alighted recently in a situation stimulating alertness.

VOCALIZATIONS

Males were recorded giving the six principal vocalizations used by both sexes, more frequently than were the females. The Musical and *Too-leet* calls were observed only in males, and the Rattle and possibly the *Ow* were restricted to females.

Vocalizations were generally most frequent in March and April, when most of the jays were in the courtship and preincubation phases of the reproductive cycle. The *Tee-ar* was the only exception, and reached a peak frequency a month or two earlier than did the other calls. There was a slight increase in vocal and reproductive activity on warm sunny days in July and August, followed by the period of least vocal and reproductive activity from October through January.

The Song was subdued in volume and characteristic of the male in courtship, but also given by both sexes when mildly disturbed after resting or while foraging. Turning of the head from side to side during the Song imparted a ventriloquial quality to it. In the group of calls characterized by low or moderate crest angles (modes 20-40 degrees) the Musical (male) and Rattle (female) were the most frequently used in supplanting and in direct threats at individual jays. Gutturals were common, but not in supplanting. Growls were uncommon, but a high proportion of them were used in supplanting.

The calls within the group characterized by high crest angles (mode 70 degrees)

could be arranged in order of decreasing frequency of association with attack as follows: *Shook*, *Wah*, *Too-leet*, *Tee-ar*.

Although Rattles and Musicals were frequently used during courtship, they were used apparently as an aggressive response toward mates or other pairs, rather than as a purely sexual response. Practically the only call used in mobbing perched owls was the *Wah*; other calls used in mobbing groups of jays were generally given at jays rather than at the owl. *Shook*'s were given in response to hunting accipitrine hawks or flying owls. On several occasions the quality of the *Shook*'s enabled the observer to predict successfully the presence of accipitrine hawks.

Reactions of a jay upon hearing a vocalization or seeing a display were often more dependent on the dominance relationship between the two jays at that site than on the nature of the call or display. Therefore, the calls and displays often did not act as releasers, but served to concentrate attention on the active jay and to emphasize the existing or potential dominance relationship. The *Shook* sometimes caused other jays and small passerines to take cover quickly. The *Wah* often attracted other jays either to an owl or to a food source, but it could also repel.

Variation between individuals in pitch, syllabification, and frequency of use of Musicals was conspicuous. Variation between individuals in frequency of use of *Too-leet*'s was also conspicuous, the call being common among the jays in the southern part of the study area and virtually absent among the jays in the northern part. Variation between local populations in the syllabification of some calls, especially those with a whistled quality, appeared to be common but could not be well documented. In contrast to the situation in *Garrulus*, as reported, mimicry in the Steller's jay was rare.

INTEGRATION OF AGONISTIC BEHAVIOR

The term "integration" with reference to behavior is used in the sense of the coördination of effector units. Attention is focused on the biological integrative properties of the nervous system as opposed to the physical and chemical internal and external stimuli responsible for behavior. A principal assumption of the method of interpretation of behavior used explicitly in this paper, and implicitly by other authors, is that when the functional type of behavior remains the same but its intensity increases, the activation of a population of neurons common to all the elements of that functional group of behavior patterns also increases. Brain-stimulation experiments support the validity of this assumption, but caution must be exercised in its use.

Three primary types of criteria for recognition of activation of specific neuro-behavioral mechanisms (NBM's) are discussed and used: (1) presence of component elements of the definitive or related acts, (2) temporal proximity of the definitive or related acts, and (3) presence of contexts typically associated with the definitive or related acts.

Use of these criteria for the Steller's jay is shown to lead to contradictory conclusions. For instance, *Shook* was both the most frequent call during aerial chasing (attack) and during flight from the bander's hand (escape). Such difficulties can be overcome with the use of other data; nevertheless, they suggest that extreme caution is required in attempts to characterize particular behavior patterns in

terms of a combination of attack mechanisms and escape mechanisms. Indeed, in this study, the more data became available, the less heuristic such attempts became.

Information on the general organization of agonistic behavior derived from brain-stimulation experiments in the cat and the hen, supports the concept of agonistic arousal, but it is ambiguous with respect to the attack-escape theory.

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PLATES

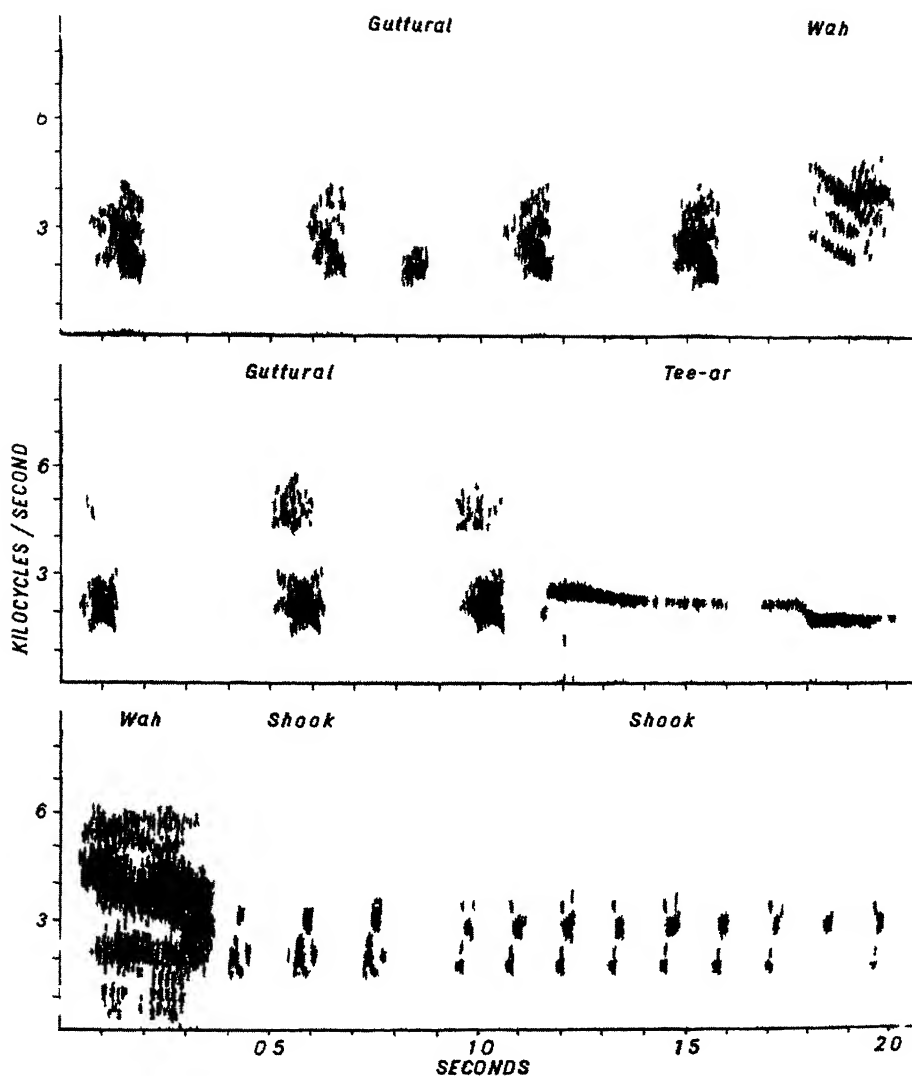


PLATE 1

Sonagrams of the principal calls of the Steller's jay recorded in Tilden Regional Park, Alameda County, California, 1959. Artifacts and background noise are particularly conspicuous in the sonagrams of the Rattle, the Musical (see pl 2), and the *Tee-ar* (see above) they appear as light, vertical lines which tend to cover the entire frequency range (See explanation of sonagrams under Methods in the Introduction.)

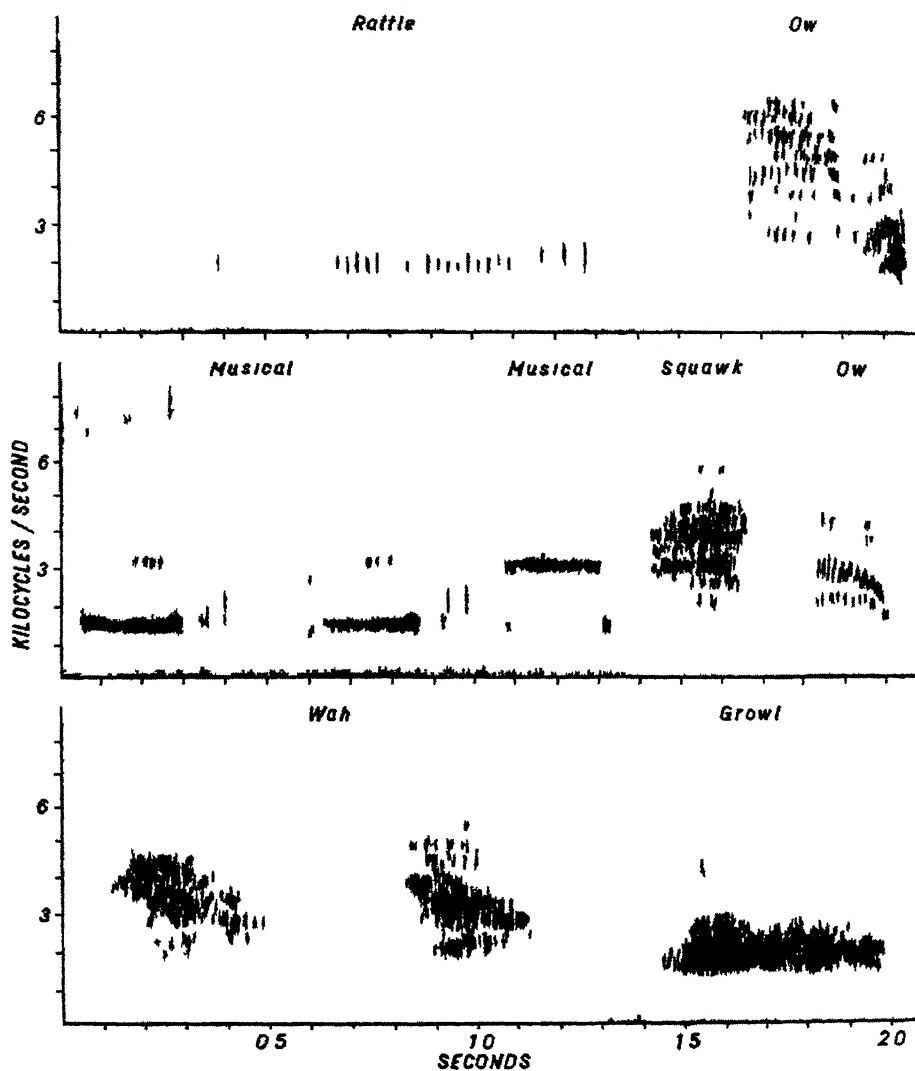


PLATE 2

Sonograms of the principal calls of the Steller's jay. The change in tone quality of the Rattle midway through the call from an 'o' to an 'ah' sound is correlated with an increase in the frequency range of the individual notes of the call. Both the low pitched 'uoot' and the high pitched 'oot' forms of the Musical are shown (see text and table 13). Note the purer tone (narrower frequency band) of the Musical and the *Tecan* (pls 1 and 2) which imparts a whistled quality to these calls.

